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ettlement of *Ostrea edulis* (L.), relation to the ultivation of oyster grounds

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Abstract

Experiments designed to evaluate the respective merits of harrowing oyster grounds or relaying shell on them in order to increase the catch of settled oyster spat are described. It is concluded that whilst the relaying of shell will result in an increase in the numbers of spat per unit area of bottom, the cleanliness of the shell is unimportant, though care must be taken to avoid introducing predators if freshly-dredged shell is laid on a new ground. Harrowing did not result in an increase in settlement per unit area of bottom and, furthermore, it was shown to have a long-term adverse effect on the growth of the oysters damaged by the harrows. Changes in the distribution of settled spat in successive years on the Rivers Crouch and Fal are discussed and possible reasons for this advanced.

Of the various types of shell relaid, those of *Ostrea edulis*, *Chlamys varia* and *Mytilus edulis* were equally suitable for spat attachment; the shells of the latter, because they are more friable and the spat on them can be separated more readily, are likely to be the most useful in practice. Other shells, such as those of *Cardium edule* and *Venerupis aurea*, are of little use, probably because their surface area is too small.

Examination of the spat on the shells and of their general distribution in relation to the numbers of shells available has shown evidence of aggregation of spat which could be attributed to gregarious settlement, though it is suggested that in nature this may be secondary to the streaming or aggregation of the planktonic larvae. On the Fal, spat settlement in relation to the presence of other sedentary organisms was also studied and it was found that in general there was a positive relation between the abundance and variety of sedentary fouling forms and the abundance of the settled spat.

Limited observations on spat survival indicate that post-settlement mortality is of the order of 93 per cent after 12 months.

Notes are included of the distribution of the molluscan fauna of Parson's Bank in the River Fal.

troduction

t of the experiments

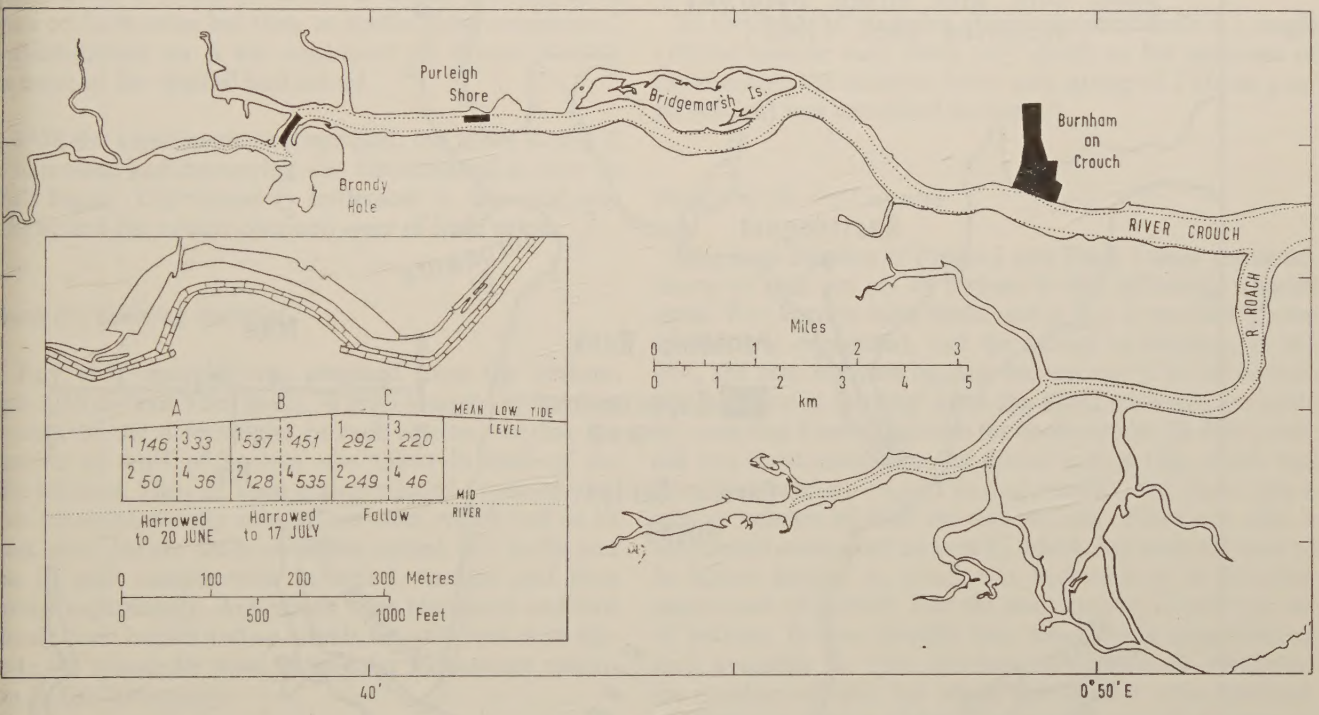
ster larvae will only settle and metamorphose if they ttach themselves to hard surfaces, and it is therefore cepted principle of oyster culture that such surfaces d be made available for spat attachment during the ment season. In regions where high-density settlement e anticipated, and where casual labour is plentiful and vely cheap, it can be economically worthwhile to set rtificial collectors—as has been done in France and nd. However, in Holland in recent years and in nd too, but on a smaller scale, it is customary to lay shell (cultch) for spat collection. As an alternative in nd, the practice has been to harrow grounds, with the t of turning shells over, killing epifauna and exposing surfaces.

e object of the experiments described here was pri- ly to test whether harrowing would result in an in- ed spatfall, and subsequently to evaluate the relative ts of harrowing and laying shell.

The character of the grounds

The first experiments, conducted in 1956, 1957 and 1958, were made on the Ministry's oyster ground at Purleigh Shore in the River Crouch (Figure 1). This ground had been leased by the Ministry in 1948 and had been reasonably well worked. It is in an area of the River Crouch where, in a good year, spatfall is likely to be most intense. The bottom is of mud overlaid by old shells of oysters and *Crepidula fornicata* and carrying also living members of both species, the latter being the dominant mollusc on the ground.

The second experiment was conducted in 1961 and 1962 on a marked area of ground in the River Fal (Figure 2). Here the bottom is of sandy mud with a scattered covering of shells—mainly of *Ostrea edulis*, *Chlamys varia*, *Venerupis pullastra* and *Venerupis aurea*—and their living counterparts. The bottom is fairly uniform and covered by water to a depth of $1\frac{1}{2}$ m at low water of spring tides.



1 Sketch map of the River Crouch, showing the location of the Purleigh Shore oyster ground, and (inset) the diagram- c layout of the experimental plot and the spatfall per m^2 in late July 1957.

sons for the choice of sites

he Purleigh Shore ground in the River Crouch was en because it was one of the Ministry's own grounds was in an area where spatfall was most likely to occur. ever, spatfall has been unreliable in the Crouch (Waugh) and proved to be so in the years 1956–58. It was con- ed, therefore, that any further experiments should be ucted in an area where a more reliable spatfall could be ipated. The River Fal is a source of natural oysters in little or no cultivation is carried out except in some of ide creeks, but observations since 1949 had shown that gh spatfall had varied considerably it had never been a re. That part of the fishery between Malpas in the north a line joining Messack and Pencarrow Points in the south is administered by the Truro Corporation under a Regulating Order which empowers them to make by-laws designed to conserve and maintain an adequate stock of oysters on the fishery. Dredging is limited and there is no cultivation in the accepted sense, but if a fairly simple method of increasing the yield from the fishery could be devised then this could probably be adopted without too much difficulty by the Corporation. The experiment on the Fal therefore had a two-fold object, firstly to determine the best way of obtaining an increased yield of spat, and secondly to demonstrate, on the spot, how this might be achieved. The Parson's Bank site of approximately 10 acres (4.04 hectares) was chosen because it was part of a substantial area of level uniform bottom which was not intensively dredged but on which a spatfall could be expected.

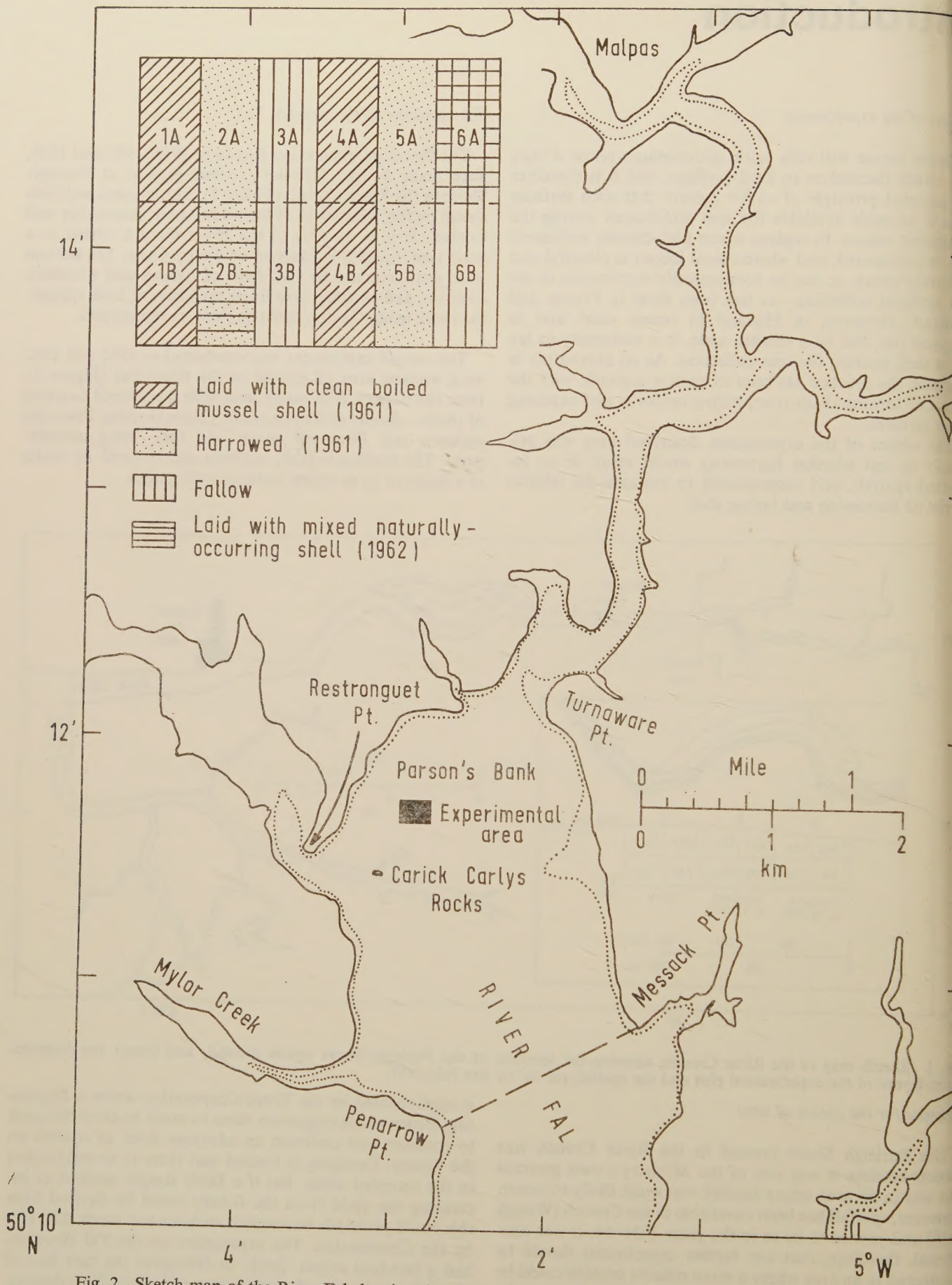


Fig. 2 Sketch map of the River Fal showing the extent of the regulated fishery (from the broken line to Malpas) a the location of the Parson's Bank site, and (inset) the diagrammatic layout and treatment of the various sections the experimental plot.

Erratum: For Penarrow Pt. read Pencarrow Pt.

xperiments in the River Crouch

t and treatment of the ground

e Purleigh Shore ground, which is about 360 m long 0 m wide, was divided into three approximately equal ns of about 120×90 m (Figure 1, inset), the divisions defined by pairs of shore marks. Each of these three ns was subsequently divided by buoys and withies into tangles approximately 60×45 m for ease in defining ions when grab sampling. In the early spring of 1956 hole area was harrowed in order to make the ground el as possible and in early April 50 000 Brittany oysters scattered over it. In mid-May, the middle and eastern ns (B and C) were harrowed for one day per week with avy agricultural harrow. The intention was to harrow til spatfall was about to take place and to continue owing C during the spatfall period. However, spatfall negligible in 1956 and the experiment was abandoned e end of July.

mid-May 1957, harrowing was recommenced, this time reas A and B. It was continued at weekly intervals up to ne on both areas but then, as spatfall had commenced, discontinued on A but continued on B until 17 July n most of the spatfall had ceased.

1958 the experiment was repeated, but areas A and C harrowed and harrowing was discontinued as soon as fall began. Unfortunately settlement in this year was light and the results obtained were of little value.

hods of collecting material

n July 1957 material was obtained from the bottom, g a 1/10 m² van Veen grab; 10 grab samples were taken n each of the 4 rectangles in each section, so that the ivalent of 4 m² of bottom was taken in each of the ted sections. The van Veen grab produced a considerable of material, mostly sub-surface mud, which had to be hed away before shells could be sorted. All shells and nes in each sample were collected, washed and then mined superficially. Any which were blackened and had iously been buried and so unable to catch spat were dis-ded; the remainder were bagged for subsequent exami-ion in the laboratory.

n October 1957 and in 1958, a Baird ½ m² grab was used description, see Baird 1958*a*) and 4 samples were taken ach rectangle so that 8 m² of bottom was sampled from n treated section. The Baird grab had the advantage that mple could be lifted with the ½ m² of bottom exposed with the majority of the shells lying in position on the d surface. These could be picked off the sample as it ne aboard, so that again only material which could have n in a position to catch spat was selected. A few shells e forced into the mud of the sample by the closing jaws he grab; once the surface layer had been removed, the ainder of the material was hosed through a coarse-hed sieve and any other suitable shells picked out.

n addition to grabbing, dredge samples were taken of the ters in each section. The native population was of mixed and origin, but the Brittany oysters which had been laid in 1956 were readily distinguishable and these were selected and measured to find out whether the harrowing had affected growth.

Method of examination

All the shells brought back to the laboratory were examined for spat under oblique light, with a x3 lens. The numbers of spat on each type of surface were recorded and at the same time the approximate volume of shell material was measured by shaking it into a graduated container.

Shells were examined dry because it is in this condition that the spat show up clearly; the raised umbone of the newly-attached spat catches the light. There remained the possibility that harrowing during spatfall could have caused excessive mortality. However, only complete spat were counted and could therefore have only been recently dead, for the right valve quickly becomes detached.

In the July 1957 samples, the numbers of shells in a single 1/10 m² sample were often very small, so for purposes of examination the material from each group of 5 (from ½ m² of bottom) was examined as one lot.

Results of the 1957 surveys

The inset diagram of Figure 1 and Table 1 show the abundance of spat per m² of bottom in the differently treated areas. Two surveys were made, one in July immediately after spatfall was completed, and the second in October. In the first, the area sampled in each section was 4 m² of bottom material, but in October when the Baird grab was available the area was 8 m² of bottom for each section. In July, spatfall was most intense on the centre section (B), which had been harrowed up to and during spatfall, but there was a greater volume of shell on this section. There was also a substantial settlement on area C, which had been allowed to lie fallow. Section A, which was harrowed up to the commencement of spatfall, had the least number of spat per m² of bottom. It was thought that the varying quantities of shell available for spat attachment might have influenced the numbers of spat, but when these figures were corrected to standard volumes of shell, the spatfall was still highest on B and least on A (Table 2).

The ground was re-surveyed in October 1957, when the result obtained using the Baird grab and sampling double the area of bottom showed that the number of spat per unit area was still greatest in the centre section but very similar on sections A and C. This pattern was repeated when the spatfall was corrected to equal volumes of shell (Table 2). Furthermore, the numbers of spat on A were substantially greater than had appeared from the July survey (Table 1).

TABLE 1 *River Crouch experiments: total numbers of spat counted in grab samples taken from Purleigh Shore; the me count per m² on each section is also shown*

A: Harrowed to 20 June				B: Harrowed to 17 July				C: Fallow			
Section	Grab sample number	Number of spat*	Mean number of spat per m²	Section	Grab sample number	Number of spat*	Mean number of spat per m²	Section	Grab sample number	Number of spat*	Mean numb of spa per m²
Late July 1957											
1A	1– 5	120	146	1B	1– 5	326	537	1C	1– 5	166	292
	6–10	26			6–10	211			6–10	126	
2A	1– 5	5	50	2B	1– 5	79	128	2C	1– 5	24	249
	6–10	45			6–10	49			6–10	225	
3A	1– 5	28	33	3B	1– 5	323	451	3C	1– 5	109	220
	6–10	5			6–10	128			6–10	111	
4A	1– 5	23	36	4B	1– 5	319	535	4C	1– 5	18	46
	6–10	13			6–10	216			6–10	28	
Overall mean number of spat per m²			66				413				202
October 1957											
1A	1	10	70	1B	1	83	127	1C	1	90	179
	2	93			2	61			2	183	
	3	22			3	49			3	82	
	4	16			4	61			4	4	
2A	1	4	30	2B	1	53	346	2C	1	39	116
	2	35			2	242			2	60	
	3	13			3	82			3	47	
	4	8			4	315			4	86	
3A	1	259	246	3B	1	92	286	3C	1	75	74
	2	46			2	202			2	28	
	3	22			3	218			3	40	
	4	166			4	61			4	6	
4A	1	41	102	4B	1	27	119	4C	1	45	53
	2	68			2	101			2	7	
	3	43			3	43			3	15	
	4	53			4	67			4	40	
Overall mean number of spat per m²			112				220				106

* In July, number in $5 \times 1/10$ m² samples; in October, number in $\frac{1}{2}$ m² sample.

TABLE 2 *River Crouch experiments: the numbers of spat on shells only and the volumes of shell material taken from Purleigh Shore. The numbers of spat which might have been expected to settle on a standard volume of shell (0.10 m³) are also shown*

A: Harrowed to 20 June

Section	Grab sample number	Shell volume (m³)	Number of spat	Corrected number of spat per 0.10 m³ shell
July 1957				
1A	1– 5	0.040	79	197
	6–10	0.020	26	130
2A	1– 5	0.010	1	10
	6–10	0.060	27	45
3A	1– 5	0.035	19	54
	6–10	0.020	1	5
4A	1– 5	0.030	13	43
	6–10	0.060	9	15
Total		0.275	175	
Mean spat per 0.10 m³ of shell				62
October 1957				
1A	1	0.05	9	18
	2	0.07	88	126
	3	0.03	22	73
	4	0.03	16	53
2A	1	0.03	4	13
	2	0.05	13	26
	3	0.05	7	14
	4	0.05	7	14
3A	1	0.08	237	296
	2	0.05	41	82
	3	0.05	22	44
	4	0.05	162	324
4A	1	0.07	21	30
	2	0.08	51	64
	3	0.08	36	45
	4	0.05	43	86
Total		0.87	779	
Mean spat per 0.10 m³ of shell				82

B: Harrowed to 17 July

Section	Grab sample number	Shell volume (m³)	Number of spat	Corrected number of spat per 0.10 m³ shell
1B	1– 5	0.050	312	624
	6–10	0.060	193	322
2B	1– 5	0.085	60	71
	6–10	0.065	42	65
3B	1– 5	0.070	322	460
	6–10	0.060	121	202
4B	1– 5	0.100	233	233
	6–10	0.060	197	328
		0.550	1 480	
				288
1B	1	0.03	81	270
	2	0.03	61	203
	3	0.03	49	163
	4	0.03	60	200
2B	1	0.08	38	47
	2	0.05	213	426
	3	0.07	69	99
	4	0.07	268	383
3B	1	0.05	87	174
	2	0.08	197	246
	3	0.07	211	301
	4	0.04	51	127
4B	1	0.04	7	17
	2	0.05	72	144
	3	0.08	41	51
	4	0.05	55	110
		0.85	1 560	
				185

C: Fallow

Section	Grab sample number	Shell volume (m³)	Number of spat	Corrected number of spat per 0.10 m³ shell
1C	1– 5	0.040	155	387
	6–10	0.040	116	290
2C	1– 5	0.060	9	15
	6–10	0.070	209	299
3C	1– 5	0.025	105	420
	6–10	0.045	87	193
4C	1– 5	0.060	11	18
	6–10	0.050	27	54
		0.390	719	
				210
1C	1	0.04	68	170
	2	0.05	163	326
	3	0.05	72	144
	4	0.01	2	20
2C	1	0.08	33	41
	2	0.07	34	49
	3	0.05	38	76
	4	0.08	29	36
3C	1	0.05	71	142
	2	0.01	25	250
	3	0.02	39	195
	4	0.01	5	50
4C	1	0.05	18	36
	2	0.05	6	12
	3	0.05	11	22
	4	0.05	25	50
		0.72	639	
				101

Living *Ostrea* and *Crepidula*, as will be shown later, catch more spat than an equivalent area or volume of their shells. Separate counts were made of the spat on them during the two surveys and the results are summarized as follows:

	Sections		
	A	B	C
	July		
Number of live oysters	31	70	57
Number of spat	37	131	41
Mean spat/oyster	1.2	1.9	0.7
Number of live limpets	395	232	355
Number of spat	53	40	49
Mean spat/10 limpets	1.3	1.7	1.1
	October		
Number of live oysters	71	103	109
Number of spat	44	68	79
Mean spat/oyster	0.6	0.7	0.7
Number of live limpets	973	658	1 367
Number of spat	76	129	129
Mean spat/10 limpets	0.8	2.0	0.9

Spat on limpets in both cases showed the highest density in the centre section B, with similar intensities on A and C. In July the mean number of spat per oyster was also highest on B but in October the differences were slight and the density of spat was similar in all three cases. On both occasions the number of oysters found was least on section A, suggesting that the observed spatfall may indicate a pattern of settlement which has taken place over several years.

Results of the 1958 survey

By comparison with 1957, the 1958 spatfall was meagre, only about a tenth of that which settled in 1957; interpretation of the results, based on the same area of material sampled, was inconclusive. The ground was not surveyed until after the end of September and, as spatfall had taken place in August, the observations were largely of survival after spatfall. The results, in Table 3, show that there was no clear indication of any change brought about by harrowing. The differences in intensity of set between the sections were insignificant, though there appeared to be a slight indication of a change in distribution of spatfall in this season, because there were as many, if not more, spat settling per unit area on the upstream section A compared with the downstream section C, a reversal of the situation which obtained in 1957. Certainly there was no indication that leaving the centre section unharrowed had resulted in a reduction in spatfall.

General distribution of spat on shells

Preliminary observations in 1950 (Waugh 1956) had shown that, volume for volume, mussel shells caught substantially more spat than cockle shells, and the possibi that some types of naturally-occurring shell might ca proportionately more spat than others was considered. Ta 4 shows the numbers of oyster, cockle and limpet sh which were found with one or more spat in the 1957 surve Apparently the oyster shells, with at least 4 times the surfa area, did not catch 4 times as many spat as the limpet cockle shells. However, though no records were kept it w apparent that a far higher percentage of the latter two fail to catch any spat. Planning the laying of shell, and t economic advantages of using varying types, could therefo be important and the further observations that were su sequently made on the Fal were done with this in mind.

Growth of the oysters

As already mentioned, Brittany oysters were laid o the whole of the Purleigh Shore experimental area in t spring of 1956, and at the same time some were laid another ground, Brandy Hole, in the upper reaches of t River Crouch. Though there was no spatfall that year, ra dom samples of oysters were dredged from each of the thr sections and from Brandy Hole in October and again November. These oysters were measured and their conditi estimated by the method of Baird (1958*b*); though there w no difference in the condition, the measurements of d meter showed that harrowing had interfered with sh growth. In October the harrowing had been completed months previously but the oysters on the harrowed sectio B and C were significantly smaller ($P=0.01$ and 0.001 spectively) than those on the unharrowed section A and Brandy Hole. In November the differences were still a parent ($P=0.01$ and >0.001 respectively) but, in additio those on the centre section B were slightly but significan bigger ($P=0.02$) than those on section C, indicating t possibility of some local environmental factor resulting rather better growth on B than on C (Table 5).

In 1957, sections A and B were harrowed and in this ye the oysters on A and C, each of which had been harrow in one year only, were similar in size ($P=>0.01$) whi those on section B, harrowed in both years, were significan smaller. During each of the two years, the percentage i crease in diameter of the unharrowed oysters was more th double that of those which had been harrowed. The resul summarized in Table 5, include the variance of each samp which was used in calculating the significance of the d ference between the large sample means.

Loosanoff and Nomejko (1955) have shown that oyst can repair damaged shell edges very quickly, but it appear from the present trials that harrowing could have a lon term effect on the oysters' growth. Thus harrowing stocked grounds in order to increase spatfall would have be carefully considered and the possibility of increased sp fall weighed against long-term interference with the grow of the oysters.

TABLE 3 *River Crouch experiments: the number of spat collected per ½ m² grab sample from Purleigh Shore in October 1958, the number of spat on shells only and the number which might have been expected to settle on a standard volume (0.10 m³) of shell*

Section	Grab sample number	Shell volume (m³)	Number of spat	Spat on shells	Corrected number of spat per 0.10 m³ shell
1A	1	0.085	30	22	26
	2	0.045	17	12	27
	3	0.050	4	3	6
	4	0.025	0	0	0
2A	1	0.050	1	1	2
	2	0.050	9	8	16
	3	0.030	2	2	7
	4	0.060	1	0	0
3A	1	0.020	5	5	25
	2	0.045	8	6	13
	3	0.035	16	14	40
	4	0.020	1	1	5
4A	1	0.135	22	18	13
	2	0.060	7	7	12
	3	0.070	10	7	10
	4	0.035	1	1	3
Total		0.815	134	107	
Mean spat per m²			17		
Mean spat per 0.10 m³ of shell					13

Section	Grab sample number	Shell volume (m³)	Number of spat	Spat on shells	Corrected number of spat per 0.10 m³ shell
1B	1	0.030	7	5	17
	2	0.060	4	4	7
	3	0.030	4	2	7
	4	0.050	7	5	10
2B	1	0.035	13	11	31
	2	0.095	9	8	8
	3	0.030	2	2	7
	4	0.040	19	18	45
3B	1	0.040	6	4	10
	2	0.030	5	4	13
	3	0.035	5	5	14
	4	0.015	0	0	0
4B	1	0.050	5	4	8
	2	0.045	15	13	29
	3	0.030	15	13	43
	4	0.050	7	7	14
		0.665	123	105	
			15		
					16

Section	Grab sample number	Shell volume (m³)	Number of spat	Spat on shells	Corrected number of spat per 0.10 m³ shell
1C	1	0.040	6	4	10
	2	0.010	4	4	40
	3	0.040	17	14	37
	4	0.030	7	4	13
2C	1	0.050	5	4	8
	2	0.040	4	2	5
	3	0.040	4	2	5
	4	0.060	5	4	7
3C	1	0.025	3	3	12
	2	0.030	3	2	7
	3	0.020	4	3	15
	4	0.005	0	0	0
4C	1	0.035	5	5	14
	2	0.030	0	0	0
	3	0.050	8	6	12
	4	0.025	3	0	0
		0.530	78	57	
			10		
					11

TABLE 4 *River Crouch experiments: the numbers of shells of different types which bore one or more spat and which were sampled on each section of Purleigh Shore. The numbers of spat on the shells and the mean spat settlement per shell are also shown*

Section	Oyster shells		Cockle shells		Limpet shells		Section	Oyster shells		Cockle shells		Limpet shells		Section	Oyster shells		Cockle shells		Limpet shells	
	Number with spat	Number of spat	Number with spat	Number of spat	Number with spat	Number of spat		Number with spat	Number of spat	Number with spat	Number of spat	Number with spat	Number of spat		Number with spat	Number of spat	Number with spat	Number of spat	Number with spat	Number of spat
July 1957																				
1A	22	62	0	0	15	31	1B	48	227	97	227	16	43	1C	19	47	64	135	35	86
2A	12	21	0	0	7	7	2B	19	73	3	3	18	26	2C	35	118	18	27	22	71
3A	6	9	0	0	7	10	3B	44	150	117	236	21	61	3C	20	46	30	64	31	71
4A	2	2	0	0	17	20	4B	72	225	43	100	37	98	4C	5	9	5	10	14	19
Total	42	94	0	0	46	68		183	675	260	566	92	228		79	220	117	236	102	247
Mean spat per shell		2.24		0.00		1.48			3.69		2.18		2.48			2.78		2.02		2.42
October 1957																				
1A	29	64	12	15	20	27	1B	60	150	31	37	16	21	1C	53	112	35	52	57	108
2A	2	2	0	0	26	27	2B	114	286	25	30	140	245	2C	27	47	5	5	58	80
3A	76	191	65	93	87	124	3B	73	169	194	220	69	92	3C	20	53	32	53	15	23
4A	11	29	5	5	79	113	4B	42	92	12	12	49	66	4C	16	21	0	0	35	38
Total	118	286	82	113	212	291		289	697	262	299	274	424		116	233	72	110	165	249
Mean spat per shell		2.42		1.38		1.37			2.41		1.14		1.55			2.01		1.49		1.51

TABLE 5 *River Crouch experiments: mean diameters of samples of relaid Brittany oysters in October and November 1956 and November 1957, and the percentage increase in diameter related to the type of treatment. Percentage increases in diameter of oysters left fallow in each season are shown in bold type. The original mean diameter (sample of 200) was 62.7 mm*

Section	1956 treatment	October (sample 100)			November (sample 200)			1957 treatment	September (sample 200)		
		Diam. (mm)	Variance	% increase on original diameter	Diam. (mm)	Variance	% increase on original diameter		Diam. (mm)	Variance	% increase on Nov. '56 diameter
Purleigh Shore											
A	Fallow	66.0	32.330	**5.3**	67.7	32.612	**8.0**	Harrowed	70.4	37.164	4.0
B	Harrowed	63.7	29.756	1.6	66.0	31.479	5.3	Harrowed	68.2	39.379	3.3
C	Harrowed	63.2	25.895	0.8	64.7	29.058	3.2	Fallow	71.9	45.849	**11.1**
Brandy Hole	Fallow	66.5	32.376	**6.1**	67.3	41.854	**7.3**				

xperiments in the River Fal

out and method of marking the ground

he area selected, measuring 183×219 m, was divided 6 strips, each 36.5×183 m, running north and south roximately parallel to the direction of tidal flow. For venience these are referred to as 1–6 from west to east gure 2, inset).

he north-east and north-west corners of the plot were rked with dahn buoys and flags, and cross-checked inst shore marks. Then, using a pair of equal marked s from these, the geometric centre of the plot was marked h a buoy and sinker. From this the south-east and south-t corners were marked off and small buoys and sinkers e then dropped along the northern and southern edges 6.5 m intervals to define the limits of the strips. A similar of buoys was dropped in an east-west direction across middle of the plot in order to divide each strip into a thern section (A) and southern section (B). These strips e necessarily long and wide because of the need for noeuvring boats within them when laying shell and har-ing.

he ground was marked out at the beginning of June and, r treatment had been completed, was left until early tember when the grab survey was made. It was important t the marks should all remain in position throughout the ole period of the experiment, and there was a danger that buoys and sinkers would be dragged out of position by d forming round them or by small boats fouling them ing the summer holiday season. By diving and linking blocks on the bottom with tightly-stretched nylon line l then cutting away the buoys and buoy lines, this danger s obviated. In September, when the time came for the b survey, it was possible to locate a line on the bottom l to swim along it, attaching a buoy to each block as it s encountered. In two 2-hour dives it was possible to re-ach all 21 buoys and have the ground re-marked in its ginal form. The same technique was used successfully the owing year, so that the marks were maintained through-t in almost the precise position in which they were origi-ly laid. Only two were moved during the period, pre-nably by boats crossing the ground when the tide was y low.

atment of the ground

n late June 1961, after the ground had been marked out, strips, numbers 1 and 4, were laid at high density, equi-ent to 30 tons per acre (75 000 kg per hectare), with clean led mussel shell from a bottling factory. Two more strips, nd 5, were harrowed intensively for a week with a heavy icultural harrow designed to bite into the bottom and lift l disturb the shells on it and in it. The remaining two ps, 3 and 6, were allowed to remain fallow. In addition 000 young oysters were scattered as uniformly as possible r the whole area in order to augment the natural popula-n on the ground.

he original plan had been to lay fresh mussel shell and compare the spatfall on this with the spatfall on the har-ed and fallow grounds. Then, in 1962, this was to be followed up with a second laying of fresh mussel shell, the settlement on which would have been compared with the settlement on the year-old shell. Unfortunately it proved impossible to purchase mussel shell in 1962 and the second part of the experiment was therefore modified. Old, naturally-occurring shell from another part of the fishery (Messack Point) was relaid instead. This mixed shell, complete with epifauna and flora, was dredged during early June and relaid at the end of each day on two half sections 2B and 6A of the experimental area until a density equivalent to 50 000 kg per hectare had been achieved on each. No harrowing was attempted in the second year. After the preparation in June, marker buoys were removed as before and the ground left until the beginning of September, when it was re-buoyed and a fresh grab survey was made.

Method of collecting, examining and recording the material

The Baird $\frac{1}{2}$ m^2 grab was used for all the bottom surveys in both years. In 1961, 10 samples were taken at random from each half of each strip, so that 10 m^2 of bottom material were removed from each strip; in 1962, at least 15 $\frac{1}{2}$ m^2 samples and, where opportunity permitted, up to 20 were taken from each half (Figure 3).

The general procedure for dealing with material was similar to that adopted for the Crouch experiments. All shell material collected was washed and examined superficially aboard the boat, and any shells which obviously could not have caught spat, because they had been buried, were discarded. The remainder were bagged and returned to the laboratory for examination. In 1962, all the material was washed through a $\frac{1}{4}$ inch (6 mm) mesh sieve and examined for living molluscs, which were recorded separately.

As before, each shell was examined for spat under oblique light through a ×3 lens. The spat of *O. edulis* and saddle oysters (*Anomiacea*), which are superficially similar, are readily distinguishable because of their different attitudes of attachment. The number and type of shells found in each sample was recorded and, in addition to counts of spat, the dominant sedentary organisms on the shells were noted. These organisms were *Pomatoceros triqueter*, Anomiids, *Verruca stroemia* and *Balanus improvisus*, and various marine algae which were not separately identified except *Lithothamnion calcareum*. No attempt was made to count these but simply to record their presence on each individual shell or settlement surface. When counting the spat, their occurrence on the outside or inside of each shell examined was recorded. Generally the insides of shells seemed to offer more suitable places for attachment, but this was not always so.

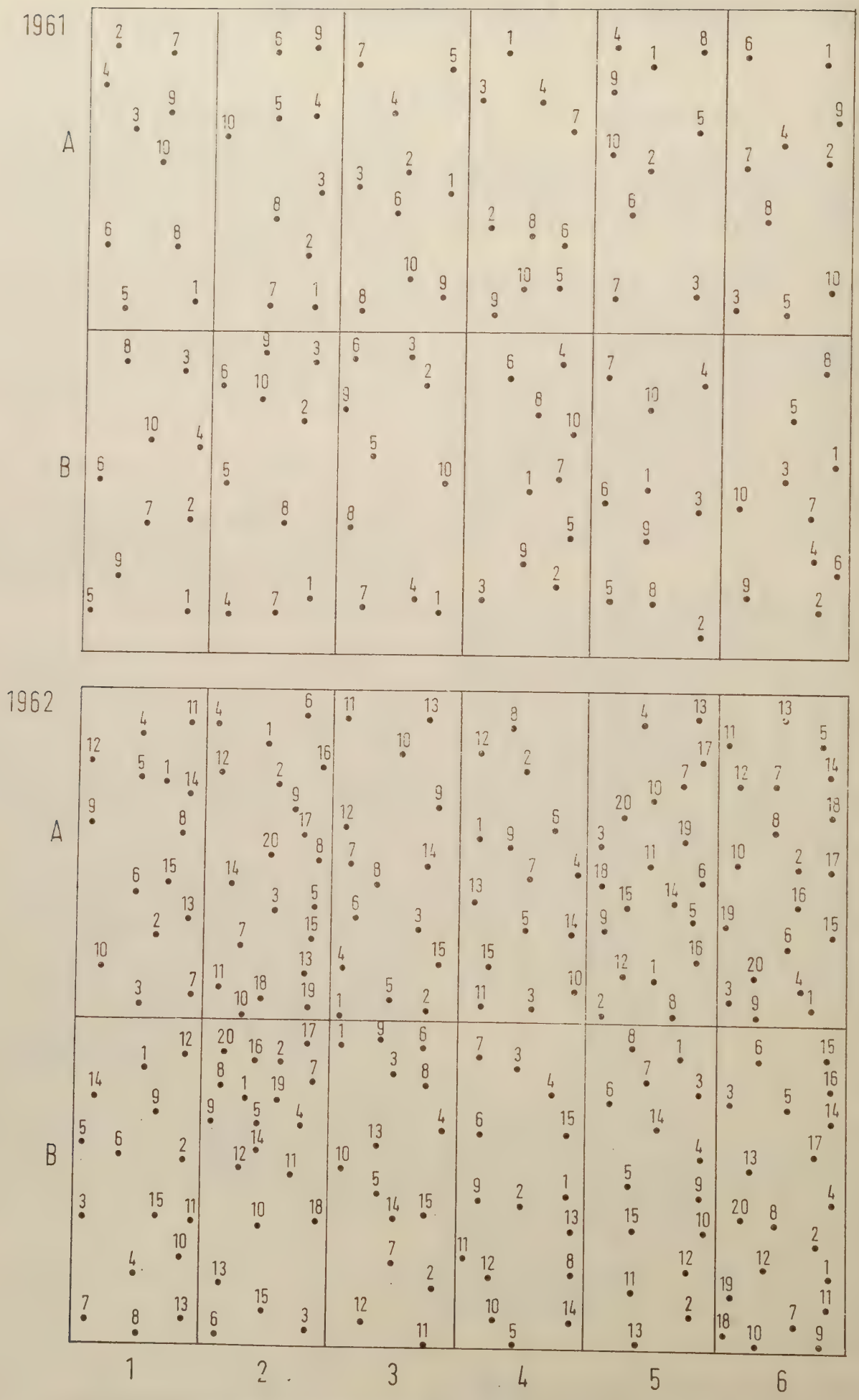


Fig. 3 Approximate positions of the grab sampling stations in the River Fal in 1961 and 1962.

ts of the 1961 survey

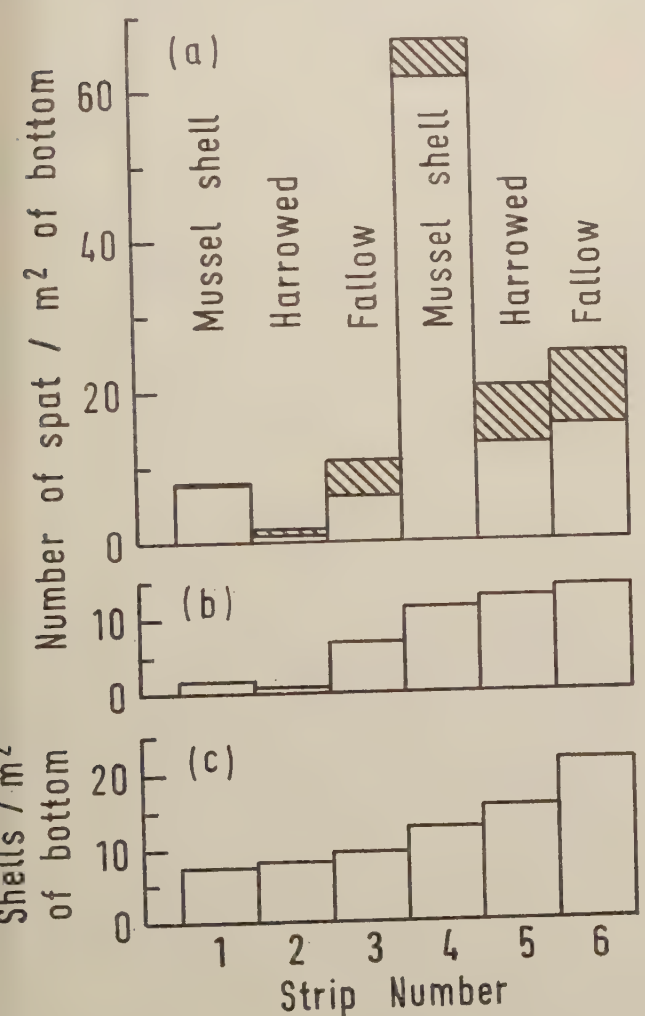
e actual numbers of spat which occurred in each $\frac{1}{2}$ m^2 sample are shown in Table 6*a* and the average settle- per m^2 on each strip is shown in Figure 4*a*. The most ng feature of the settlement was the greatly increased ber of spat per m^2 of bottom on the mussel-shell-treated , 4. Although settlement on strip 1, also laid with mussel , was greater than on the adjoining harrowed strip 2, ffect of the presence of the shell was less apparent. The rences observed in spatfall per unit area of bottom on arly treated sections were apparently due to a basic de- se in settlement across the width of the plot from east est. This is shown in Figure 4*b* where the spatfall on oduced mussel shell has been excluded from the data. t this difference is probably a normal feature of the area dicated in Figure 4*c*, where the numbers of old oyster ls per unit area of bottom are illustrated and show a lation in numbers similar to that observed for spatfall. observation of the distribution of oyster shell was ely confirmed on the 1962 survey (see Table 11*b*).

nder normal circumstances the decrease of spatfall ards the west could be attributed either to lack of suit- surfaces for attachment, or to absence of larvae. A re- tion in the area of suitable surfaces, as will be shown later, had little effect on the numbers of spat which settled on those surfaces that were present. The spatfall failure on the west side, despite a plentiful supply of mussel-shell surfaces, suggested either that there were fewer larval oysters available for settlement from the water on that side, or that conditions for settlement were less suitable, for example, possibly the period of slack water was shorter. In order to discover whether the results could be interpreted in any other way, the area of shell surface available for settlement was also considered.

Random collections of the shells typically found in the samples were laid on paper and their outlines traced. The areas of these tracings were then measured using a planimeter and from the results an average plan area for each type of shell was obtained. Some shells had obviously been partly buried in the substrate and offered only a small area for spat attachment, whilst others had apparently been held above the substrate and offered parts of both sides for attachment. However, in considering spatfall on the shells and for the purposes of obtaining an approximate figure for the shell surface, it was assumed that the area available was equivalent to the plan area, i.e. to one side only, of each shell.

Using these figures for area, the average spatfall on shells and the total area of these shells was calculated so that the mean spatfall could be expressed in relation to shell area available per m^2 of bottom. These figures were then recalculated according to a standard area of shell (Table 7). It will be seen from this that apparently even if there had been a plentiful supply of shell over the whole area there would still have been a gradation from west to east across the area, but with an abrupt change in intensity to the east of strip 2.

If the different treatments are considered separately, it is seen that the spatfall per unit area of bottom on the mussel-shell-treated strips, 1 and 4, was significantly greater than on the adjacent harrowed strips 2 and 5 ($P=0.01$ and 0.001 respectively). Thus the addition of the mussel shell had resulted in a much increased set per unit area. Harrowing, however, did not result in an increased settlement; in fact the spatfall per unit area on the harrowed strip 2 was less than on the fallow strip 3 and also less on the harrowed strip 5 than on the fallow strip 6. As has already been mentioned, the area of shell available for spat attachment was apparently not increased by harrowing.



g. 4(a) Numbers of spat/m^2 on the treated strips in 1961, with spat on oysters shown cross-hatched.

b) Numbers of spat/m^2 on the treated strips in 1961, exding those which settled on mussel shells.

c) Numbers of old oyster shells/m^2 recovered from the ated strips in 1961.

TABLE 6 *River Fal experiments: numbers of spat found in each grab sample in 1961 and 1962 and the mean numbers per m² on each treated strip. Figures are for total spat, including those on live oysters and* Chlamys

Section	Treatment	Grab sample number																				Total	Mean number per m²
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		
		(a) Number of spat in 1961																					
1A	Mussel shell	3	2	0	1	0	12	1	4	2	0											25	5.0
1B	,,	7	0	1	3	9	3	14	1	4	8											50	10.0
2A	Harrowed	0	0	0	0	1	0	0	2	0	0											3	0.6
2B	,,	2	0	0	0	1	0	0	5	0	0											8	1.6
3A	Fallow	2	0	2	0	3	0	33	34	2	0											76	15.2
3B	,,	4	0	0	3	14	0	8	0	0	0											29	5.8
4A	Mussel shell	81	4	1	74	30	41	54	58	24	19											387	77.4
4B	,,	0	32	9	1	61	36	23	71	20	20											273	54.6
5A	Harrowed	1	15	23	6	1	2	15	20	26	4											113	22.6
5B	,,	4	13	6	0	0	10	25	5	23	1											87	17.4
6A	Fallow	19	15	1	22	6	1	0	21	11	3											99	19.8
6B	,,	17	9	57	20	0	2	11	2	27	0											145	29.0
		(b) Numbers of spat in 1962																					
1A	Mussel shell	42	16	2	25	36	89	28	30	65	109	3	1	17	36	18						517	68.9
1B	,,	105	62	16	10	32	88	28	100	70	104	106	24	269	79	169						1 262	168.3
2A	Fallow	3	22	67	1	22	17	35	29	19	3	79	0	84	6	91	12	30	1	10	0	531	53.1
2B	Old shell	31	78	81	13	266	344	49	40	172	22	33	110	78	215	90	50	178	16	27	5	1 898	189.8
3A	Fallow	1	36	34	3	0	1	3	14	16	0	8	9	0	9	40						174	23.2
3B	,,	2	34	15	9	1	9	1	60	2	46	2	84	1	0	23						289	38.5
4A	Mussel shell	126	47	31	35	102	40	59	11	34	42	45	15	57	39	39						722	96.3
4B	,,	15	137	28	105	154	351	68	181	28	54	98	161	40	34	85						1 539	205.2
5A	Fallow	14	0	3	2	134	19	76	3	44	28	16	18	16	52	1	34	32	14	53	54	613	61.3
5B	,,	85	2	13	1	43	20	18	1	22	3	3	5	0	86	56						358	47.7
6A	Old shell	311	64	57	59	70	79	8	8	128	11	15	14	101	147	9	15	16	128	305	7	1 552	155.2
6B	Fallow	7	9	3	6	3	40	17	11	15	74	17	28	44	8	19	5	27	17	49	15	414	41.4

TABLE 7 *River Fal experiments: the calculated area of shell sampled from each section in 1961 and 1962, and the approximate area of shell surface (cm²) per m² of bottom. Total spatfall and spatfall corrected to 1 000 cm² of shell are also shown*

Strip and section	Treatment	Area of bottom covered (m²)	Area of shell sampled (cm²)	Mean shell area (cm²) per m²	Number of spat	Calculated number of spat per 1 000 cm² of shell	Mean spat per 1 000 cm² of shell
	(a) 1961 experiment						
1A	Mussel shell	5.0	41 586	8 317	25	0.6	1.3
1B	,,	5.0	24 625	4 925	49	2.0	
2A	Harrowed	5.0	1 799	360	3	1.7	2.0
2B	,,	5.0	1 708	342	4	2.3	
3A	Fallow	5.0	2 080	416	46	22.1	15.4
3B	,,	5.0	1 965	393	17	8.7	
4A	Mussel shell	5.0	27 491	5 498	372	13.5	13.9
4B	,,	5.0	17 043	3 409	243	14.3	
5A	Harrowed	5.0	4 442	888	77	17.3	17.0
5B	,,	5.0	3 014	603	50	16.6	
6A	Fallow	5.0	4 219	844	69	16.4	17.7
6B	,,	5.0	4 243	849	81	19.1	
	(b) 1962 experiment						
1A	Fallow	7.5	26 813	3 575	461	17.2	21.5
1B	,,	7.5	37 148	4 953	957	25.8	
2A	Fallow	10.0	6 169	617	248	40.2	50.4
2B	Old shell	10.0	20 352	2 035	1 231	60.5	
3A	Fallow	7.5	4 227	564	110	26.0	30.4
3B	,,	7.5	4 479	597	156	34.8	
4A	Fallow	7.5	29 894	3 986	619	20.7	30.8
4B	,,	7.5	35 549	4 740	1 455	40.9	
5A	Fallow	10.0	8 119	812	307	37.8	47.4
5B	,,	7.5	5 480	731	312	56.9	
6A	Old shell	10.0	21 795	2 180	1 007	46.2	39.0
6B	Fallow	10.0	9 708	971	310	31.9	

Results of the 1962 survey

The spatfall in 1962 was much more intense than in 1961. The numbers of spat found in each grab sample and the mean settlement per m² of bottom are shown in Table 6*b* and illustrated in Figure 5. Direct comparison of spatfall for 1962 with that of 1961 could not be made by combining the northern and southern sections of each strip, but when spatfall was related to the area of shell available for settlement there still appeared to be a tendency for settlement to be slightly less on the west side of the area. The spatfall calculated according to a standard area of shell, as for 1961, is shown in Table 7*b*; this illustrates that the overall settlement was more intense and more evenly distributed in 1962.

The addition of old shell to the north end of strip 6 and the south end of strip 2 had resulted in a considerable increase in the spatfall per unit area of bottom on these two sections compared with that on the adjacent untreated grounds. However, there was relatively little difference between the settlement per unit area on those strips to which mussel shell had been added in 1961 (1 and 4) and the two sections to which the old shell was added in 1962 (6A and 2B).

The occurrence of fouling forms

The shells which occurred naturally on the bottom bore a variety of sedentary organisms both before and after the experiment, but the mussel shells, when laid, were clean or at the most bore empty barnacles and the tubes of *Pomatoceros triqueter*. It was therefore possible to obtain some data on the relative settlement of species other than oysters on these shells.

The dominant fouling organisms which settled in 1961 were *Pomatoceros triqueter* and *Anomia ephippium* (L.). Barnacles, mainly *Verruca stroemia*, settled relatively sparsely in 1961 but in 1962 all three species were common. No attempt was made to count these species but, in the majority of samples, as each mussel shell was examined for spat, the presence of algae and the other fouling species on the whole shells and also on the pieces of shell was noted.

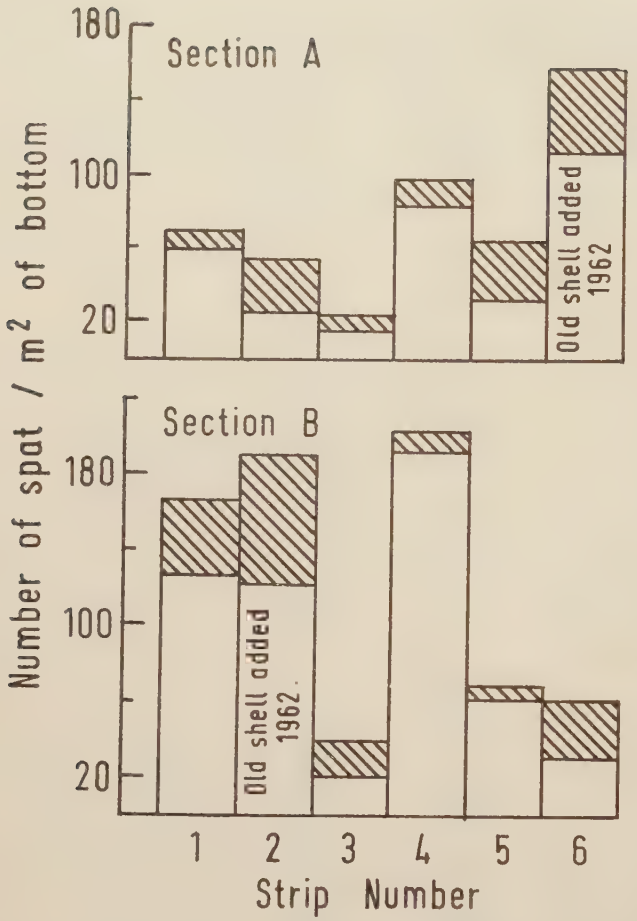


Fig. 5 Numbers of spat/m² on the northern (A) and southern (B) sections of the treated strips in 1962, with the spat on oysters shown cross-hatched.

In order to determine whether the presence of these species affected spatfall, the settlement on whole mussel shells from strips 1 and 4 was examined separately. In Table 8 the number of shells examined in this way is shown, subdivided according to the type of fouling present. *Pomatoceros* alone or in combination with other species was present on the majority of the shells. In general those shells which carried mixed fouling, i.e. *Pomatoceros*, *A. ephippium* and barnacles, as well as algae, caught the highest percentage of settling spat whilst, conversely, the lowest percentage was caught by those shells which bore only encrusting or filamentous algae and small forms, i.e. those that were 'cleanest'. The actual numbers of spat settling on the shells varied considerably and there appeared to be little difference in their numerical abundance on the differently fouled shells (Table 8).

Cole and Knight-Jones (1939, 1949) showed that lightly-fouled surfaces were most suitable for spat collection under tank conditions, and Waugh and Ansell (1956) showed that under natural conditions heavy fouling with barnacles will impede or reduce spat settlement. In the Fal experiments fouling of the mussel shells by the larger species was relatively light, with seldom more than four *Pomatoceros* tubes per shell. It seems probable that this fouling was insufficient materially to affect spat settlement, but rather that it was an indication that the shell surface, the lack of silt, or its angle of presentation, was particularly suitable for the attachment of sedentary animals, including oyster spat. Certainly those shells with mixed fouling caught the highest percentage of the spat which settled (Table 8). Thus it seemed that the provision of clean, bleached, shell for spat collection was not of great importance in the Fal. Certainly the old, fouled shell gathered from Messack Point in 1962 proved very successful for spat settlement, though it was much 'dirtier' than the mussel shell.

On strip 4 there was no significant difference in the percentage of shells which caught spat in 1962 compared with 1961, but on strip 1 the percentage increase was considerable (Table 8). As was to be expected, the average catch of spat per 10 mussel shells also showed a considerable change on strip 1 (from 0.27 to 4.61) but a lesser increase on strip 4 (from 3.01 to 5.37), a measure of the overall increase in intensity of set in the second year and of its changed distribution. In the lower reaches of the Fal, downstream of a line drawn due east from Mylor Creek, the shell on the bottom is characterized by the presence of the encrusting purple alga *Lithothamnion calcareum*, which did not occur on Parson's Bank. In 1962 the material dredged from Messack Point contained a fairly high proportion of shells encrusted with this alga. It was not present in 1961 on any of the mussel shells on the experimental ground but it had colonized some of the shells by September 1962. The degree of fouling was relatively light and it was noticeable that it was less on the inshore strip 1 than on the offshore strip 4:

Section	Number of whole shells examined	Number with *Lithothamnion*	% affected
1A	508	10	2.0
1B	908	50	5.5
Total	1 416	60	4.2
4A	578	38	6.6
4B	764	56	7.3
Total	1 342	94	7.0

It is possible that the slightly muddier conditions inshore interfered more with the development of the alga there. It is questionable whether the species will become established in the area but continuing observations will be made to determine this.

Associated fauna

In 1961 the presence of living molluscs, including oysters, in the surface deposits brought up by the grabs was recorded but no attempt was made to sort the material systematically for other species. In 1962, after the surface material had been removed from the sample, the residue was hosed through a sieve with $\frac{1}{4}$ inch (6 mm) mesh and living species were picked out.

The mean densities per m² of the species which occurred most commonly in the grab samples are shown in Table 9. The figures for burrowing forms are minimal because the grab was designed to take mainly surface material and, as Birkett (1957) points out, the numbers found are related to the volume of material grabbed.

The first and most striking observation was the presence of *Ocenebra erinacea* in the sections 2B, 6A and 6B in 1962. This species had not been found in 1961 and its presence had not been recorded in the area during the course of general dredge surveys made in the previous 5 years. The animal was however present on the rough ground close to Messack

BLE 8 *River Fal experiments: the numbers of whole mussel shells examined and the type of fouling on them, together with the numbers of shells bearing oyster spat and the numbers of spat on these shells, and the percentage of fouled shells which caught spat; the percentages fouled by different organisms, and the percentage distribution of the spat in relation to fouling, are also shown*

	Type of fouling					Total
	Weed and small forms	*Pomatoceros* only	Anomia only	Barnacles only	Mixed fouling	
ip 1, 1961						
Number of shells	373	535	87	–	277	1 272
Number with spat	3	10	0	–	18	31
% with spat	0.8	1.9	0.0	–	6.5	2.4
Number of spat caught	4	10	0	–	20	34
Mean number of spat per shell	1.3	1.0	0.0	–	1.1	
% of total shells fouled	29.3	42.0	6.8	–	21.7	
% of total which caught spat	9.7	32.3	0.0	–	58.1	
% of total spat caught	11.8	29.4	0.0	–	58.8	
ip 1, 1962						
Number of shells	505	540	37	44	290	1 416
Number with spat	40	108	8	12	97	265
% with spat	7.9	20.0	21.6	27.3	33.4	18.7
Number of spat caught	79	235	31	26	282	653
Mean number of spat per shell	2.0	2.2	3.9	2.2	2.9	
% of total shells fouled	35.7	38.1	2.6	3.1	20.5	
% of total which caught spat	15.1	40.8	3.0	4.5	36.6	
% of total spat caught	12.1	36.0	4.7	4.0	43.2	
rip 4, 1961						
Number of shells	307	405	111	–	378	1 201
Number with spat	43	85	12	–	113	253
% with spat	14.0	21.0	10.8	–	29.9	21.1
Number of spat caught	57	125	20	–	160	362
Mean number of spat per shell	1.3	1.5	1.7	–	1.4	
% of total shells fouled	25.6	33.7	9.2	–	31.5	
% of total which caught spat	17.0	33.6	4.7	–	44.7	
% of total spat caught	15.7	34.5	5.5	–	44.2	
rip 4, 1962						
Number of shells	551	419	66	49	257	1 342
Number with spat	44	97	17	15	96	269
% with spat	8.0	23.2	25.8	30.6	37.4	20.0
Number of spat caught	95	200	85	31	310	721
Mean number of spat per shell	2.2	2.1	5.0	2.1	3.2	
% of total shells fouled	41.0	31.2	4.9	3.7	19.2	
% of total which caught spat	16.4	36.1	6.3	5.6	35.7	
% of total spat caught	13.2	27.7	11.8	4.3	43.0	

oint from which most of the old cultch had been collected. As many of these rough tingles as possible had been removed by culling through each dredge catch and, in the ourse of gathering the cultch, 506 *Ocenebra* and approximately 600 000 egg capsules were collected and destroyed. Nevertheless, substantial numbers must have been laid with he cultch to give the population density observed. It is noteworthy also that *Ocenebra* had apparently moved very little uring the period June to September, in that it still appeared o be confined to 2B when sampling was begun and it had nly spread slightly from 6A. Single specimens were found n section 6B in grab samples 6 and 15, the two taken earest to the southern side of 6A (Figure 3).

Observations on the Messack Point ground, from which ysters were absent, suggested that *Ocenebra* was feeding rimarily on *Venerupis aurea* and *Venerupis pullastra*, but on he experimental area a few drilled oyster shells were observed in September 1962.

These observations emphasize the necessity for adequate control when transplanting shell. Though as many tingles as possible were removed during the catching of the cultch, enough were left to materially affect the ultimate catch of oysters from the spat settling on the relaid cultch. Orton (1929) referred to the feeding of *Ocenebra* from Falmouth on oysters. Hancock (1960) found that *Ocenebra* took 6–7 days to consume a small oyster and 9–10 to eat a medium-sized one. He also cited observations by Cole (pers. comm.) who found that *Ocenebra* from the Helford River consumed 0.2 oyster spat per day. On 2B, where the density of the snail was 0.7 per m^2, this would be equivalent to the removal of 0.14 spat per m^2 per day, and, during the 6 or so months when the snails are active, a consumption of 25 spat per m^2. Thus the beneficial effects of laying cultch in order to catch spat could clearly be negated if too many predators were added at the same time.

TABLE 9 *River Fal experiments: the mean density per m² of the most commonly occurring species on the different sectio of the experimental plot in 1961 and 1962. Note the increased numbers of oysters introduced with the old cultch 1962 (indicated by *)*

Species	Section											
	1A	1B	2A	2B	3A	3B	4A	4B	5A	5B	6A	6B
	(a) Grab samples taken in 1961											
Ostrea edulis	0.60	1.00	0.20	1.00	1.40	0.60	2.40	2.40	1.60	1.40	1.20	5.0
Chlamys varia	0.20	0.20	–	–	0.20	–	1.20	0.60	–	0.40	0.60	0.4
Mytilus edulis	–	–	–	–	–	–	–	–	–	0.20	0.40	–
Venerupis pullastra	1.20	1.80	0.20	0.20	0.20	0.20	0.80	0.80	1.40	0.40	0.60	0.2
V. aurea	7.00	7.60	2.40	1.20	0.80	0.80	7.40	4.80	2.20	0.80	0.80	0.2
Nassarius reticulatus	–	–	–	–	–	–	–	–	0.20	–	0.40	–
	(b) Grab samples taken in 1962											
Ostrea edulis	1.33	4.67	2.20	11.40*	1.20	1.07	2.00	1.20	3.20	1.33	7.50*	1.2
Chlamys varia	0.67	1.07	0.50	1.70	0.40	0.27	0.27	1.20	0.50	0.40	2.80	0.3
Mytilus edulis	–	0.13	–	–	0.13	–	0.53	0.40	0.60	–	–	–
Venerupis pullastra	0.13	0.40	0.40	0.70	0.40	0.40	1.06	1.60	0.60	0.27	1.20	0.2
V. aurea	3.87	6.40	9.40	6.40	2.67	3.33	6.27	6.13	6.20	5.33	8.30	4.6
Cardium edule	0.13	–	0.10	–	–	–	–	–	0.10	0.13	–	–
C. exiguum	1.20	0.67	4.10	2.40	1.47	1.20	1.33	2.00	2.40	0.93	2.00	1.2
Nassarius reticulatus	0.13	–	0.60	0.10	0.93	0.40	0.53	0.13	0.20	0.13	–	0.5
Ocenebra erinacea	–	–	–	0.70	–	–	–	–	–	–	0.30	0.2
Crepidula fornicata	–	–	–	0.10	–	–	–	–	–	–	0.20	–

Crepidula fornicata was not present on Parson's Bank in the 1961 samples though its shells were fairly common, mixed with the mussel shells which were relaid. However, this species has become less and less of a rarity in Cornish estuaries since it was first recorded in 1946 (Cole 1952), and can be found in a number of places in the Fal. Its presence off Messack Point is demonstrated by its inclusion in the dredged material relaid on 2B and 6A. It was only on these two sections that living *Crepidula* were found in the two series of grab samples in 1961 and 1962.

Of the other species occurring on the ground, the commonest was undoubtedly *Venerupis aurea*, the shells of which predominated in the majority of the grab samples. The species exhibited very little change in density from one part of the experimental area to another and, though the physical character of the substrate varied slightly, with an increasing amount of mud from east to west, the animal seemed adapted to this range of conditions. So too did th allied species *Venerupis pullastra* which, though common was not of large size, seldom exceeding 3.5 cm in length.

Cardium edule was uncommon on Parson's Bank and th majority of the individuals found were small and less tha two years old. *C. exiguum* on the other hand, which i typical of muddy oyster grounds in Essex (Mistakidis 1951) was widely distributed and numerically abundant, an showed little difference in density of population from eas to west on the area.

Other species whose presence was noted were two speci mens of *Laevicardium norvegicum*, and *Kellia suborbicular* which was common in the empty shell valves ('clocks') o *Venerupis pullastra*; there were often up to six individual per clock.

iscussion

differences in intensity of spatfall in the River Crouch in 7 and 1958

here was a considerable difference in the intensity of lement on the experimental area in the River Crouch in 7 and 1958. Average spatfall per m² of bottom in 1958 14, whereas in 1957 it was 145, i.e. rather more than 10 es as intense. Routine plankton samples taken in the er Crouch during the two summer seasons gave averages 5 eyed larvae per 100 litres during 1957 and 0.3 per 100 s in 1958, i.e. larvae ready to settle were approximately times as abundant in 1957 as they were in 1958.

hus the difference in intensity of settlement over the area a whole was primarily due to very different survival and wth of the larvae in the two different seasons, rather than differential survival of the spat. The spatial distribution the settled spat in the two years is less easy to interpret ause of the wide difference in intensity and the relatively samples taken. Nevertheless, there appears to have been ifference in the distribution in the two years, with pro-rtionately more spat settling on the downstream section 1957 than in 1958. In this experiment the differently-ated sections were along the axis of the river and therefore vae ready to settle would presumably be transported over e section after another. This makes the differences in ensity of settlement less easy to understand, except in ms of the variability of the bottom and the shell surface as available for attachment.

e difference in intensity of spatfall in the River Fal in 1961 d 1962

The mean number per m² of bottom of oyster spat which ttled on the shells of *Ostrea edulis*, *Chlamys varia*, *Mytilus ulis*, *Venerupis pullastra*, *Venerupis aurea* and *Cardium ule* in the sections other than 2B and 6A, which received ecial treatment in 1962, was 19.2 in 1961 and 59.8 in 1962. pparently there was a three-fold increase in intensity of ttlement in the second year. However, the quantities of ell taken in the two seasons in each sample varied slightly, ut from Table 7 (where the combined total area of shell ken from each section is shown, together with the total patfall) a spatfall per 6 000 cm² of shell surface was cal-ulated. On this basis the mean number of spat per 6 000 m² of shell was 46 in 1961 and 205 in 1962, which rep-sents a more than four-fold increase in intensity.

At the time of the grab surveys, general dredge surveys ere also made over the Truro fishery from its southern mit to Malpas in the north in order to obtain information n the abundance and distribution of oyster stocks and spat-ll. In the course of the surveys, paired empty shell valves locks) were collected at random from the dredged material nd examined for spat. In 1961 the mean count was 4.2 spat er clock from 68 clocks, and in 1962 it was 16.5 from 29 locks—again a four-fold increase in intensity, though based n small samples. It appeared, therefore, that the difference n intensity of spatfall between 1961 and 1962 on the experi-ental area reflected conditions on the fishery generally, ven though the distribution of settled spat on the plot was uite different in the two years.

In 1961, settlement was lightest on the western side of the experimental area, being in some cases less than one-fifth of the settlement on a correspondingly-treated strip 120 yards (110 metres) to the east. However, in 1962, though the overall intensity was greater, the increase was most marked on the western side, where it was at least 20 times as heavy as in 1961; on the east it was only approximately double. The mean numbers of spat per shell amongst those which caught spat were very similar on each strip for the same year and, though in 1962 the mean number per shell was almost doubled, the big difference was the increase in the numbers of shells catching spat (see Table 8).

The effects of harrowing

The object of harrowing is said to be two-fold: first to pull buried shells out of the substrate, and second to turn over exposed shells, so killing (by smothering) attached sedentary organisms. In both cases there should be an increase in the area of relatively competitor-free surfaces available for spat attachment.

The first case can only apply if there are substantial quantities of shell buried in the substrate. In the case of the harrowed and fallow sections on the River Fal, there was no significant difference in the quantities of shell available on the harrowed plots—as opposed to the fallow ones—at the time of the grab survey, made approximately 8 weeks after harrowing had been completed. If the value of harrowing lies in the second explanation, then it was to be expected that the spatfall per shell on the harrowed strips would be greater than on the fallow strips. This was not the case. The same general observations apply to the River Crouch experiment where, although shells were plentiful, there was no measurable increase in the number of spat per shell on the harrowed sections.

Underwater observations in the Fal showed that it was difficult to detect any change at all in the bottom after harrowing. The amount of mud and silt stirred up by the harrows was considerable and, though harrowing was always carried out during the run of the tide, a considerable amount of the heavier material that was whirled into suspension resettled close behind the harrow on top of shells turned up by it.

The effect of strong winds was even more apparent. Attempts to observe conditions after a period of strong winds coinciding with low spring tides proved difficult because of turbidity, but later on it was apparent that a fresh thin layer of silt had been re-deposited on a high proportion of the cultch after the considerable churning the bottom had received. Thus it is doubtful if harrowing will have much beneficial effect in pulling shells from the bottom into a position where they are free to catch spat unless it is done immediately prior to spatfall, and then any good that might be done in this respect can rapidly be undone by a period of rough weather.

On the other hand oysters, which often tend to lie in depressions in the bottom, as do scallops (Baird and Gibson 1956), or are buried to the free edge of the shell, are lifted

TABLE 10 *River Fal experiments: combined area and combined weight of all shells grabbed from the different sections in 1961 and 1962, with the areas and weights of the different types expressed as percentages of the totals. In the same way, the number of spat settling on each type of shell has been expressed as a percentage of the total settlement*

Section	Shell area (cm²)	Shell weight (g)	Number of spat	*O. edulis*			*C. varia*			*M. edulis*			*V. pullastra*			*V. aurea*			*C. edule*		
				% area	% wt	% spat	% area	% wt	% spat	% area	% wt	% spat	% area	% wt	% spat	% area	% wt	% spat	% area	% wt	% spat
	(a) Samples taken in 1961																				
1A	41 586	26 422	25	1.0	1.1	0.0	0.3	0.2	0.0	94.8	96.4	92.0	1.8	1.3	8.0	1.8	0.9	0.0	0.3	0.1	0.0
1B	24 625	15 506	49	5.4	6.1	14.3	1.1	0.7	4.1	87.1	89.5	77.6	2.1	1.5	2.0	3.9	2.1	2.0	0.3	0.1	0.0
2A	1 799	987	3	51.4	67.0	33.3	11.5	7.9	66.7	1.0	1.2	0.0	11.7	9.3	0.0	23.8	14.3	0.0	0.6	0.3	0.0
2B	1 708	982	4	54.2	67.3	50.0	8.1	5.3	0.0	5.3	6.0	25.0	14.9	11.3	25.0	17.5	10.1	0.0	0.0	0.0	0.0
3A	2 080	1 180	46	51.7	65.1	87.0	8.7	5.1	10.9	5.3	6.0	2.1	17.3	13.3	0.0	17.5	10.2	0.0	0.5	0.3	0.0
3B	1 965	1 150	17	57.2	69.9	82.4	10.5	6.8	5.9	2.8	3.1	0.0	19.8	14.8	11.8	9.6	5.4	0.0	0.0	0.0	0.0
4A	27 491	17 281	372	5.6	6.3	4.0	1.7	1.0	14.5	84.8	88.0	80.1	3.3	2.3	1.3	4.0	2.1	0.0	0.7	0.3	0.0
4B	17 043	10 470	239	9.0	10.4	10.5	2.7	1.7	0.8	77.1	81.1	87.0	5.1	3.6	1.7	5.9	3.1	0.0	0.2	0.1	0.0
5A	4 442	2 369	77	43.9	58.8	68.8	7.2	5.2	3.9	2.5	3.0	2.6	21.6	17.7	23.3	24.5	15.2	1.3	0.2	0.1	0.0
5B	3 014	1 749	50	58.1	71.5	80.0	12.2	8.0	10.0	1.8	2.0	0.0	14.2	10.7	10.0	13.7	7.8	0.0	0.0	0.0	0.0
6A	4 219	2 424	69	55.1	68.5	72.5	5.5	3.6	2.9	2.6	2.9	14.5	20.3	15.4	8.7	16.5	9.5	1.4	0.1	0.1	0.0
6B	4 243	2 650	81	70.7	80.9	84.0	7.6	4.6	1.2	3.0	3.1	3.7	8.8	6.2	11.1	9.9	5.2	0.0	0.0	0.0	0.0
Total	134 215	83 170	1 032																		
Mean (%)				38.6	47.7	48.9	6.3	4.2	10.1	30.7	31.8	32.1	11.7	9.0	8.6	12.4	7.2	0.4	0.2	0.1	0.0
	(b) Samples taken in 1962																				
1A	26 813	16 302	459	6.1	7.1	6.3	2.1	1.3	3.7	78.9	84.0	81.7	3.8	2.7	5.9	8.7	4.7	2.4	0.5	0.2	0.0
1B	37 148	23 107	955	5.7	6.6	13.0	1.6	0.9	4.6	83.8	87.3	79.3	3.0	2.1	1.2	5.0	2.7	2.0	0.9	0.4	0.0
2A	6 169	2 968	248	31.2	46.3	43.5	7.1	5.6	16.9	3.8	5.2	7.7	15.0	13.6	18.1	42.2	29.0	13.3	0.6	0.3	0.4
2B	20 352	11 893	1 231	57.7	70.6	63.5	12.7	8.2	21.3	4.2	4.7	3.7	12.0	9.0	9.7	13.3	7.5	1.7	0.1	0.0	0.0
3A	4 227	2 225	110	37.3	50.6	64.5	10.3	7.4	7.3	10.8	13.3	10.0	13.0	10.8	13.6	28.3	17.7	4.5	0.4	0.2	0.0
3B	4 479	2 188	156	35.2	49.8	56.4	5.1	4.0	17.3	0.8	1.1	1.3	24.4	21.9	14.1	34.2	23.1	10.9	0.2	0.1	0.0
4A	29 894	17 965	619	7.5	8.9	21.6	2.2	1.4	6.9	73.7	79.5	63.5	6.0	4.4	5.3	10.2	5.6	1.6	0.4	0.2	1.0
4B	35 549	21 699	1 455	7.2	8.4	13.5	1.4	0.9	1.9	77.0	81.8	73.3	6.5	4.7	8.3	7.6	4.1	2.3	0.3	0.1	0.7
5A	8 119	4 297	307	39.1	52.8	47.2	6.2	4.5	15.6	6.3	7.7	16.3	24.2	20.0	16.9	23.9	14.9	3.6	0.3	0.1	0.3
5B	5 480	2 982	310	40.6	53.3	52.6	5.5	3.8	5.5	11.0	13.1	21.0	19.0	15.3	14.5	23.8	14.4	6.5	0.2	0.1	0.0
6A	21 795	12 226	1 007	53.8	68.5	63.8	7.9	5.3	11.2	0.9	1.1	1.9	17.9	14.0	19.4	18.6	10.9	3.7	0.4	0.2	0.1
6B	9 708	5 318	306	49.4	64.5	58.8	7.8	5.4	10.1	1.3	1.5	2.0	18.4	14.7	18.0	23.0	13.9	10.8	0.1	0.0	0.3
Total	209 733	123 171	7 163																		
Mean (%)				30.9	40.6	42.1	5.8	4.1	10.1	29.4	31.7	30.1	13.6	11.1	12.1	19.9	12.4	5.3	0.4	0.2	0.2

by the harrow and re-deposited on the surface, so that his way the chances of loss due to smothering are re- d. This slight advantage can be offset, however, by the age done to the oysters, for, as mentioned earlier, this age to the growing shells is not readily repaired. ough Loosanoff and Nomejko (1955) showed that aged oysters quickly replaced shell, continuous harrow- apparently affected the rate of repair. While there was evidence from the Crouch experiments of untoward tality resulting from harrowing, there was a 50 per cent duction in the increase in diameter. This could substan- y affect the yield of a fishery.

here is nothing to be gained by attempting to encourage fall on grounds used for pre-market fattening, where the ence of new season's spat on the market oysters consti- s a nuisance. Separation of stock and spatting grounds, n within a limited area, would therefore be an advantage.

importance of shell types as spat collectors

Choice of surface for attachment by spat has been sug- ted by several workers (Cole and Knight-Jones 1949; rringa 1940; etc.); however, this does not necessarily an an active seeking out of suitable surfaces but more bably a failure, by the larvae, to attach to some. Apart m the results given by Cole and Knight-Jones, who wed aged surfaces to be important, there is little evidence t texture plays any significant part in stimulating attach- nt to hard surfaces. There is, for example, a considerable ference between the rough surface of the tiles used in nce and the smooth mussel shells used in Holland.

Cole and Knight-Jones (1949) have shown that, under k conditions, equivalent areas of oyster and cockle shells ght equivalent numbers of spat, but work on the relative ching efficiency of mussel and cockle shells (Waugh 1957) s shown that bulk for bulk the former caught many more at than the latter. It was therefore important to assess different types of shell as collectors, and for this reason spatfall on the different types of shell encountered in the urse of the Fal surveys was investigated.

The numbers of shells varied in each section and so did e relative proportions of one type to another. To compare eir relative catching efficiency the plan area of all the ells of one type encountered per section was expressed as percentage of the total area of all the shells in that section. the catching efficiencies of the shells were equal, then the rcentage distributions of the spat should have been ex- cted to be the same as, or similar to, the percentage distri- tions of the areas of the shells. Table 10 shows that the ells of *Ostrea edulis*, *Chlamys varia* and *Mytilus edulis* ere equally used for settlement, those of *Venerupis pullastra* d probably *Cardium edule* were less used, and those of *enerupis aurea* were scarcely used at all. Shells of *Crepi- la fornicata* were too few in number for their suitability to assessed.

Although it was not possible to compare 'over-year' and esh-laid' mussel shell, the relative catching efficiency of e shell in the two years showed little difference. It appeared at the suitability of this shell for spat attachment did not ange to any degree between the two seasons. In 1961 ussel shells, which occupied 30.7 per cent of the total area ailable, caught 32.1 per cent of the spat, and in 1962, hen they occupied 29.4 per cent of the area, they caught .1 per cent of the spat. It must be borne in mind, however, that other fouling forms were not particularly abundant; there was, for example, very little fouling by barnacles. On the east coast, where *Elminus modestus* is abundant (Knight-Jones 1948), such shells would probably have been more heavily fouled and so less suitable as spat collectors.

The presence of excessive numbers of shells of one type, i.e. mussel, did not apparently influence the settlement on shells of other types found in the samples. In Table 11 the numbers of shells of each type and the percentage which caught spat in 1961 and 1962 are shown. The presence of excess quantities of mussel shell in sections 1A, 1B, 4A and 4B made no apparent difference to the percentage of the other shells on which spat settled.

In considering the shapes and surface areas of the shells, it is recognized that the shells of *Ostrea* and *Chlamys* are very much corrugated, so that their actual surface area in relation to the plan area is proportionately greater than that of the shells of *Mytilus* or *Venerupis*. Spat rarely settled on the outside of the mussel shells where the periostracum was still present and, as this is easily shed in any case, it seemed probable that spat so attaching would be lost. It was, however, noticeable that no spat settled on the outside of living mussels which were, it is true, relatively uncommon. In contrast, spat settled abundantly on the shells of living *Ostrea* and *Chlamys*.

The shells of *V. pullastra* and *V. aurea* are apparently very similar in surface character but the latter caught proportionately far fewer spat than the former. It is possible that the surface area over which larvae crawl before fixation has a bearing on this and that the small size of the *V. aurea* shells has a limiting effect. Korringa (pers. comm.) came to a similar conclusion in his observation of the settlement behaviour of *O. edulis* on artificial collecting surfaces. He considered that a minimum crawling area of 6 cm^2 was required. The mean area of the *V. aurea* shells was 4.5 cm^2.

From the results obtained, it appeared that shells of oysters offered the best chance of catching spat and that those of *Mytilus edulis* and *Chlamys varia* were slightly less suitable. From a practical point of view, where freight has to be considered, the shells offering the greatest suitable surface area for a given weight would be most satisfactory, and for this reason shell weights were considered.

The average weights of the different types of shell were determined, and from these and the numbers of shells the percentage by weight of each type of shell was estimated. In the same way as for surface area, the percentage distribution of spat was related to weight of shell (Table 10). The results showed that weight for weight the shells of *Chlamys varia* caught more spat than any of the other types; that the percentage weight and percentage catch by the shells of *O. edulis*, *V. pullastra* and *M. edulis* was approximately in the ratio of 1:1, even though the shells of the latter had been laid in excess; and that the shells of *V. aurea* were unsatisfactory. Too few *C. edule* were found to give an estimate of their suitability.

Thus, on the weight basis, the shells of *C. varia* are likely to be most suitable, whilst those of oysters, mussels and *V. pullastra* come second, although again the excessive density of the mussel shell may have masked some of its efficiency. Korringa (1951a) has pointed out that relatively friable shells such as those of *M. edulis* have the advantages that they do not persist long enough to harbour pests and that spat on them can be separated easily by breaking the shell.

TABLE 11 *River Fal experiments: the numbers of shells of each type sampled on the various sections in 1961 and 1962, and the percentage which bore one or more spat*

Section	*O. edulis*		*C. varia*		*M. edulis*		*V. pullastra*		*V. aurea*		*C. edule*	
	Total shells	% with spat	Total shells	% with spat	Total shells	% with spat	Total shells	% with spat	Total shells	% with spat	Total shells	% with spat
	(a) Samples taken in 1961											
1A	16	0	5	0	2 156	1	101	2	163	0	20	0
1B	53	6	12	17	1 175	3	70	1	210	1	12	0
2A	37	3	9	11	1	0	28	0	93	0	2	0
2B	37	3	6	0	5	20	34	3	65	0	0	0
3A	43	14	7	43	6	17	48	0	79	0	2	0
3B	45	18	9	11	3	0	52	4	41	0	0	0
4A	61	25	20	30	1 287	17	120	2	237	0	34	0
4B	61	30	20	10	718	22	116	3	216	0	7	0
5A	78	31	14	21	6	17	128	13	237	1	2	0
5B	70	27	16	19	3	0	57	5	90	0	0	0
6A	93	20	10	10	6	33	114	4	151	1	1	0
6B	120	23	14	7	7	29	50	8	91	0	0	0
Total	714		142		5 373		918		1 673		80	
Mean (%)		17		15		13		4		0		0
	(b) Samples taken in 1962											
1A	65	17	24	29	1 158	12	135	9	506	1	22	0
1B	85	40	25	44	1 707	16	149	7	407	1	58	0
2A	77	39	19	58	13	54	123	10	566	3	7	14
2B	470	49	112	62	47	26	326	11	589	3	3	0
3A	63	33	19	21	25	16	73	7	260	1	3	0
3B	61	38	10	70	2	100	146	5	333	3	2	0
4A	90	33	28	36	1 209	13	239	5	663	2	21	14
4B	102	39	22	41	1 502	21	309	18	585	3	20	20
5A	127	35	22	46	28	50	262	12	422	2	4	25
5B	89	29	13	54	33	46	139	8	283	1	2	0
6A	464	45	75	59	11	73	521	16	879	4	15	7
6B	189	38	33	36	192	38	238	9	485	4	1	100
Total	1 882		402		5 927		2 645		5 944		158	
Mean (%)		36		46		39		10		2		15

Thus mussel shell seems likely to offer the best commercial form of cultch, though if ever the shells of *C. varia* became available in quantity these might be better still.

Gregariousness

Cole and Knight-Jones (1939), Knight-Jones and Stevenson (1950), and Knight-Jones (1953*a*, *b*) showed that the planktonic larvae of some marine animals, including *O. edulis*, exhibit certain preferences for settlement surfaces, and that the presence of already attached individuals of the same species will stimulate the larvae to attach. Some of the above work was done in the laboratory and most of it on specially prepared surfaces. The present work lends itself to further observations on settlement under more natural conditions.

The mussel shells provided semi-standard surfaces and the settlement on them affords good evidence of aggregation. In Figure 6 the numbers of spat settling on whole mussel shells only, on strips 1 and 4 in 1962, have been plotted as frequency histograms. Analysis of the results showed that the settlement did not follow a Poisson distribution but that the variance was considerably in excess of the mean, by factors of 5.8 and 7.7 respectively. This, according to Holme (1950) and Ursin (1960), constitutes evidence of aggregation, but this in turn would only be evidence of gregariousness if all the shells were exactly similar in texture, angle of presentation, etc.

There has been a tendency to ascribe quite local aggregations of spat, particularly on artificial collectors, to gregariousness, an active seeking out of already attached spat and adults by the larvae, but true gregarious settlement in all probability results primarily from contact stimulus. The contact must, however, come about largely by chance, because the larvae are only capable of limited directional movement under tidal conditions and would seem to be incapable of seeking out attached spat.

Therefore, in considering spatfall in relation to the surface area available for attachment, it must be appreciated that over a large area the density of settlement cannot exceed the

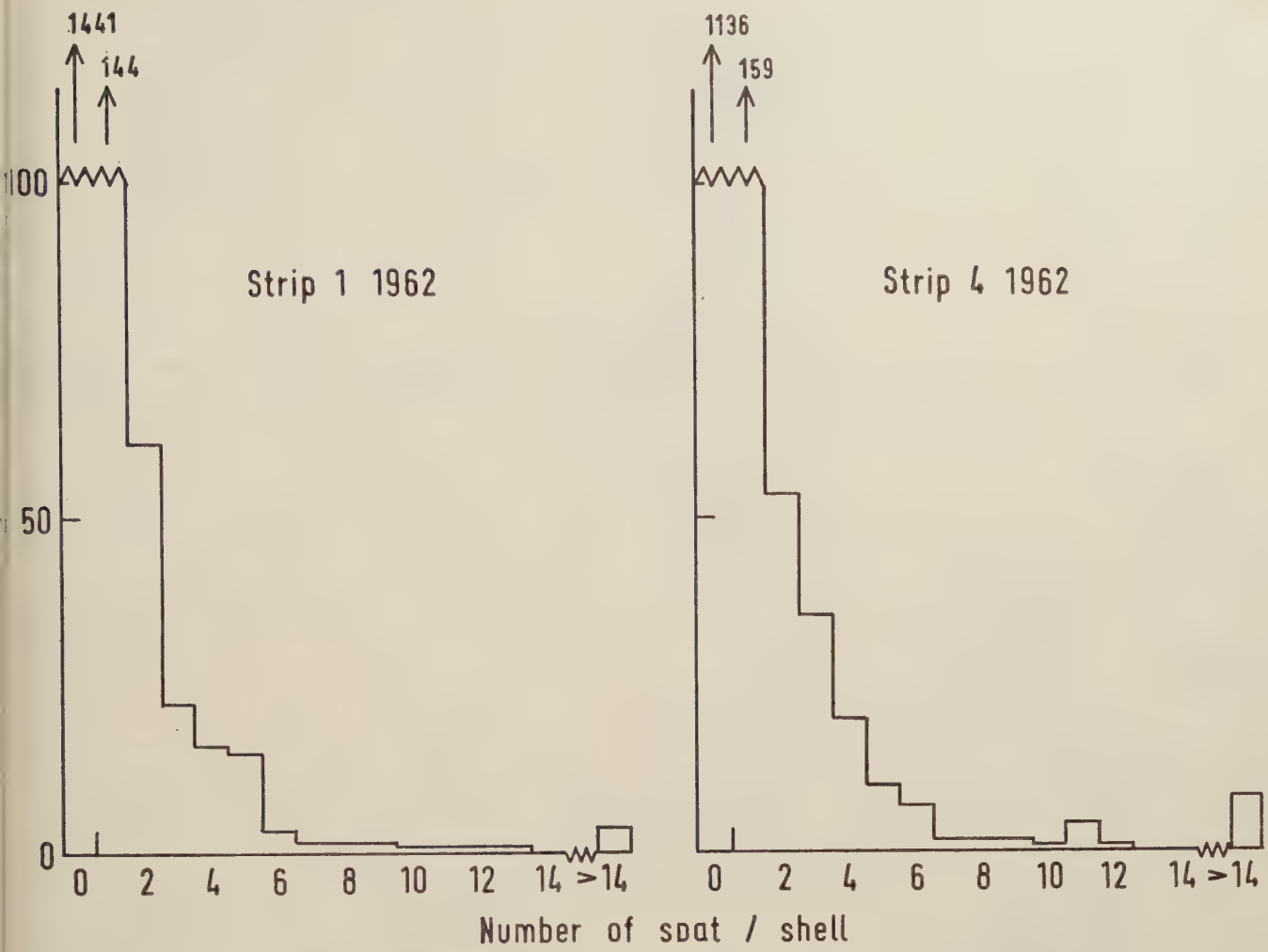


Fig. 6 Frequency distribution of spat, on whole mussel shells only, on strips 1 and 4 in 1962.

al numbers of pediveligers carried in the water over that ea. As suggested previously, there is no evidence that the at aggregate if there are only few settlement surfaces ailable on the bottom. This is borne out by the results ven in Table 12 which show that, except in the case of ussel shell which was present in excess in some sections, e mean numbers of spat per shell were essentially the same espective of whether the cultch was plentiful or sparse in e different sections. Consequently one must assume that e numbers of spat settling per unit area of bottom will be lated to the available area of shell and will be limited by e numbers of available larvae.

In Figure 7*a* and *b* the numbers of spat found per $\frac{1}{2}$ m^2 sample of bottom in 1961 and 1962 have been plotted against the log value of the estimated area of shell available in each sample. Allowing for the difficulty of defining the shell areas precisely, it is apparent that there was a maximum spatfall for each area of shell. Lines for maximum density of spat per unit area have been fitted by eye and the differing slopes in the two years illustrate the different intensities of spatfall, with the steeper slope in 1962 reflecting the heavier spatfall, and presumably the greater density of late-stage larvae. in that year.

ABLE 12 *River Fal experiments: spatfall as mean numbers of spat per shell in the different sections in 1962, subdivided according to the abundance of the shells*

ell type	Sections with plentiful cultch								Sections with limited cultch							
	Total shells	1A	1B	2B	4A	4B	6A	Mean	Total shells	2A	3A	3B	5A	5B	6B	Mean
strea edulis	1 276	0.45	1.48	1.66	1.49	1.93	1.37	1.40	604	1.40	1.13	1.44	1.14	1.83	0.94	1.31
hlamys varia	286	0.71	1.72	2.34	1.54	1.23	1.51	1.51	116	2.21	0.42	2.70	2.18	1.31	0.94	1.63
lytilus edulis	5 634	0.32	0.44	0.98	0.33	0.71	0.73	0.75	293	1.46	0.44	1.00	1.79	1.97	0.86	1.25
enerupis pullastra	1 679	0.20	0.07	0.37	0.14	0.39	0.37	0.26	966	0.37	0.21	0.15	0.20	0.32	0.33	0.26
enerupis aurea	3 629	0.02	0.05	0.04	0.02	0.06	0.04	0.04	2 315	0.06	0.02	0.05	0.03	0.07	0.07	0.05

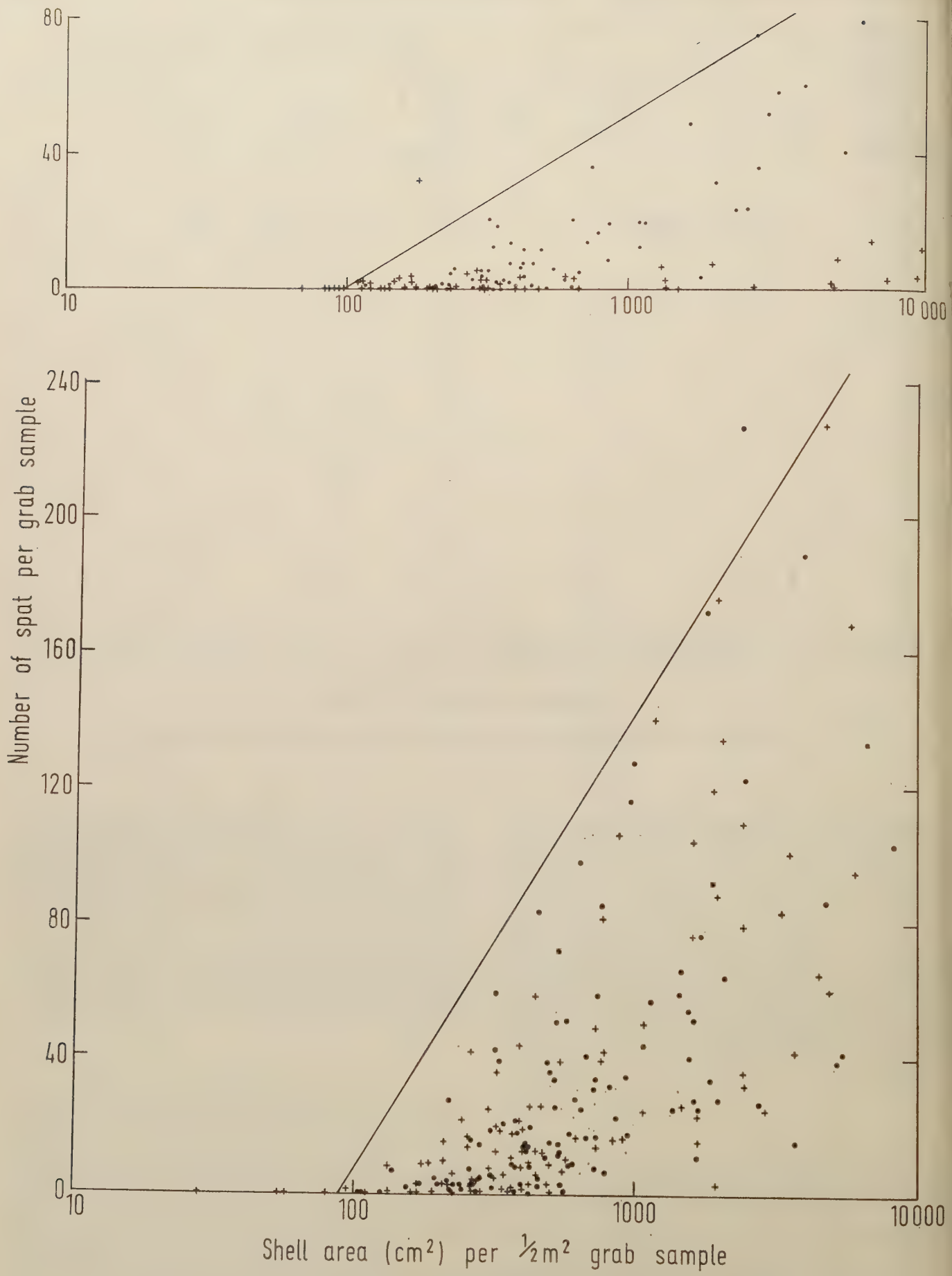
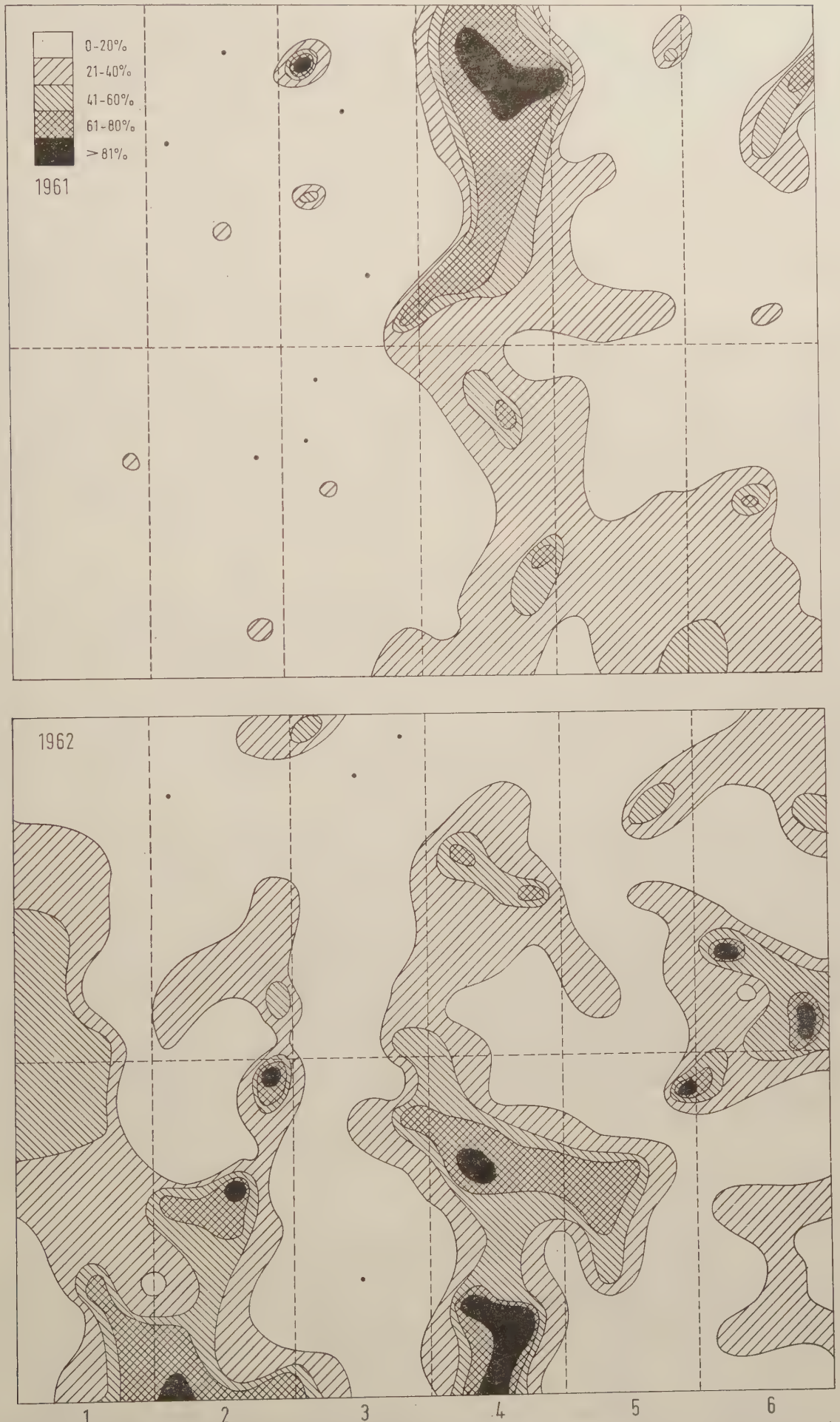


Fig. 7 Numbers of spat per $\frac{1}{2}$ m^2 grab sample which settled on shells only, plotted against $\log_{10}$ of the area of available shell surface in 1961 (above) and 1962 (below).
+, strips 1 to 3; ●, strips 4-6.



g. 8 Diagrammatic representations of the relative intensity of spatfall on the experimental plot in 1961 (above) and 1962 (below). hese have been obtained by contouring the actual settlement per $\frac{1}{2}$ m^2 expressed as a percentage of the maximum probable set rived from Figs 7(a) and (b). Solid circles indicate points of nil settlement (areas of shell too small for spat settlement).

In both years there were no spat where the shell area was less than 100 cm^2 per $\frac{1}{2}$ m^2 of bottom. It has already been suggested that the crawling larvae require a minimum searching area before they attach themselves and that the small shells of *Venerupis pullastra* and *V. aurea*, which predominated in these samples, were generally unsuitable for such attachment. The failure of the few other, larger, shells to catch spat could have been due to chance because of the relatively limited numbers of larvae in the water. Furthermore, a sufficient quantity of shell is required on the bottom to ensure that larvae sinking randomly through the water have a reasonable chance of encountering suitable surfaces for attachment.

The differences in slope of the lines of maximum possible set also illustrate the need for economy in laying shell. In 1962, a shell density of 1 000 cm^2 per $\frac{1}{2}$ m^2 could have given a yield of 140 spat, yet in 1961 10 times this shell density would only have given a yield of 105 spat. The economics of laying shell collectors, or indeed any other form of collector, therefore have to be considered in terms of the possible increase in yield. Hence, prediction of the anticipated density of settlement, as well as its timing, could be of considerable advantage to the oyster farmer.

In order to obtain an impression of the distribution of spat in the two years and to make allowances for the variability of the shell on the bottom, the numbers of spat counted per individual sample were expressed as a percentage of the maximum possible for the area of shell in that sample, using the data presented in Figure 7*a* and *b*. These percentages were then inserted on charts in place of the grab stations. Though the deviations from the maximum were considerable, there was a relationship between results for adjacent samples and these deviations could be contoured (Figure 8). In both years, there was a tendency for areas of similar relative intensity of set to run north-south, parallel with the direction of the tidal streams, and in both years there was a zone of high intensity along the length of strip 4, overlapping into 5B. In 1961, on the mussel-shell-treated strip 1 and the harrowed and fallow strips 2 and 3, the realization of the potential catch of spat was low; in 1962 there was a higher relative density of settlement on strip 1 and on 2B (treated with old shell) but there was also an area of fairly high relative set on 2A. Strip 3 was largely barren in both years. In 1962, though the realization of the potential was high on 6A (laid with old shell), there were extensions into 6B and 5A. Thus, though the results may have been partly influenced by the addition of shell, it appeared that this method of treating the results gave some indication of the sort of distribution that would have occurred had the bottom been uniformly covered with shell.

Numerous authors, including Anraku (1956), Bainbridge (1953), Crisp (1962) and Barlow (1955), have referred to swarming of planktonic organisms, and Cassie (1963) has referred to small-scale concentrations (a micro-distribution) within the large-scale distribution. In cases where the planktonic organisms are in an immediate pre-settlement stage, it is to be expected that the pattern of settlement will also be patchy and reflect the planktonic distribution. The north-south orientation of the areas of similar spatfall, and the fact that settlement took place over several days and tides, suggests some persistence in the pattern of larval distribution over the experimental area, but further work would be necessary to confirm this.

Factors influencing settlement on single shells will be their suitability for this purpose (i.e. freedom from silt, and the angle of presentation) and the numbers of larvae coming into contact with them by chance. If the shell, because of its angle, creates an eddy in its vicinity which results in the larvae being held there for longer than normal, there is a greater chance that one will settle. Others then being held in its vicinity will also be stimulated to settle. Thus, on this basis, gregarious behaviour would be very much a secondary factor causing aggregation. The secondary role played by gregariousness is further substantiated by comparison of the settlement of spat on living oysters and *Chlamys*. Table 13, which shows the numbers of spat settling on these living animals and on their corresponding shells, also shows that the living animals caught many more spat than the shells. The similarity between the catching capacity of the oysters and *Chlamys* is even more strikingly illustrated when only those animals or their shells which caught at least one spat are considered (Table 13*c*). From this it appears that the suitability of the two types of shell is almost the same and that they catch less than half as many spat as their living counterparts, both of which also show the same catching capacity. Increased settlement on living oysters could have been explained in terms of gregariousness, but increased set on the living *Chlamys* shows that there must be other explanations.

The growing shellfish, by their shell movements and feeding currents, tend to keep themselves relatively free of silt and so could offer a cleaner substrate for spat attachment. The new growing edges particularly, being free of fouling, might be expected to be most favourable for settlement, but detailed examination has shown the spat to be almost uniformly distributed over the shell surface (see Korringa 1951*b*). Nelson (1952) stated that living *Crassostrea virginica* filtered out planktonic larvae of their own species and that their larvae were capable of passing along the gills or through the gut unharmed and of being discharged in faeces or pseudo-faeces from which they subsequently escaped. He advanced the theory that this trapping of the larvae could, in some measure, explain the apparent attraction of the adult oysters for their own spat. My own observations indicate that a high proportion of the larvae engulfed by *Ostrea edulis* are re-released and swim actively, escaping from both faeces and pseudo-faeces, but this alone does not explain why spat should have been numerous on the oysters and *Chlamys* unless there was substantial trapping by both species of larvae about to settle, and unless the larvae could also pass unharmed through the gut of *Chlamys varia*. Possibly the effect of the feeding currents alone could be sufficient to set up micro-eddies over the shells which would bring more larvae into contact with them. This effect, coupled with the fact that the living shellfish tend to stand proud of the surrounding substrate, would further increase the chances of larvae coming into contact with them.

Survival of oyster spat

Incidental to the main work the present study offered an opportunity for the tentative estimation of mortality under natural conditions on the experimental areas. On the Fal, the settlement in 1961 was relatively light but some of the spat survived into 1962. In the course of the second survey, particular note was made of the presence of these one-year-old spat where it was certain that they could only have settled in the experimental area in 1961. The additional old cultch laid on sections 2B and 6A in 1962 contained some small oysters, so that the presence of one-year-old spat on

E 13 *River Fal experiments: the numbers of living* Ostrea edulis *and* Chlamys varia, *and the numbers of shells for these two species taken in grab samples in 1961 and 1962, and the numbers of spat on them*

	Strip number						Total	Mean spat per live individual or shell
	1	2	3	4	5	6		
	(a) Samples taken in 1961							
ber of living *O. edulis*	8	6	10	24	15	31	94	
ber of spat	1	4	42	36	64	88	235	2.50
ber of shells of *O. edulis*	69	74	88	122	148	213	714	
ber of spat	7	3	54	40	93	118	315	0.44
ber of living *C. varia*	2	0	1	9	2	5	19	
ber of spat	0	0	0	9	9	6	24	1.26
ber of shells of *C. varia*	17	15	16	40	30	24	142	
ber of spat	2	2	6	56	8	3	77	0.54
	(b) Samples taken in 1962							
ber of living *O. edulis*	45	136	17	24	42	86	350	
ber of spat	349	808	158	164	307	427	2 213	6.32
ber of shells of *O. edulis*	150	547	124	192	216	653	1 882	
ber of spat	155	890	159	331	308	822	2 665	1.42
ber of living *C. varia*	12	22	5	11	8	31	89	
ber of spat	11	136	39	23	34	197	440	4.94
nber of shells of *C. varia*	49	131	29	50	35	108	402	
nber of spat	60	304	35	70	65	144	678	1.69
	(c) Samples taken in 1962							
ber with settled spat								
ng *O. edulis*	43	116	15	20	38	75	307	7.21
lls of *O. edulis*	48	269	47	74	73	290	801	3.33
ing *C. varia*	7	12	4	5	5	23	56	7.88
lls of *C. varia*	18	82	11	19	18	57	205	3.31

ese two sections was not necessarily indicative of the spat ving settled on them.

In Table 14 are shown the mean numbers of spat per m^2 1961 and the mean numbers of survivors in 1962. On the stern strips, where settlement was light in 1961, the mor- ity appeared to have been less than on the east. However, e errors in estimation, where small numbers of spat were unted from variable quantities of shell, were considerable. n 4A and 4B, where settlement was most intense in 1961 d where cultch was plentiful, the estimated mortality was and 92 per cent respectively and similar to that of the her eastern sections. The total number of spat counted in 1961 was 1 296 from 60 m^2 of bottom, i.e. 21.6/m^2; in 1962, 134 survivors were counted from 82.5 m^2 of bottom, i.e. 1.6/m^2. This gives an overall mortality of 93 per cent. As already pointed out, all spat, whether alive or dead, were counted when the shells were examined and, as the left valves of spat leave a visible trace only 24 hours after metamorphosis, the estimate of spatfall must have been close to that of the total settlement. Walne (1961) reports a mortality of 85 per cent during the first year for cultured oysters on tiles, but this figure applied to spat 14 days old and more; hence it is to be expected that his estimate of mortality would be lower.

ABLE 14 *River Fal experiments: the mean numbers of newly-settled spat recorded per m^2 of bottom in 1961 and the numbers of survivors per m^2 in 1962. Sections 2B and 6A are ignored because some spat may have been introduced on to these sections with the old cultch laid in 1962*

ction	Mean spat per m^2 in 1961	Mean 1961 spat per m^2 in 1962	% mortality	Section	Mean spat per m^2 in 1961	Mean 1961 spat per m^2 in 1962	% mortality
A	5.0	1.2	76	1B	10.0	2.7	73
A	0.6	0.6	0	2B	1.6	–	–
A	15.2	0.5	97	3B	5.8	1.3	78
A	77.4	3.7	95	4B	54.6	4.4	92
A	22.6	1.7	92	5B	17.4	0.7	96
A	19.8	–	–	6B	29.0	1.2	96

TABLE 15 *River Crouch experiments: the mean numbers of newly-settled spat recorded per m² of bottom in October 195 and the numbers of the survivors recorded per m² in October 1958*

	Section														
	1A	2A	3A	4A	Mean	1B	2B	3B	4B	Mean	1C	2C	3C	4C	Mea
Mean spat per m² October 1957	71	30	247	103	113	127	346	287	119	220	180	116	75	54	106
October 1958	97	45	65	81	72	211	52	80	73	104	57	61	54	29	50
% mortality, Oct./Oct.					36					53					53

In the River Crouch, sampling was even more restricted than in the River Fal. Because of changes in technique in the early part of the study, it is only possible to make worthwhile comparisons between the samples taken in October 1957 and those of October 1958. The change in number per unit area is shown in Table 15. There was good agreement between the various sections and the results indicated that four-month-old spat were subject to an overall mean mortality of 48 per cent in the following twelve months.

These estimates of mortality can only be considered as approximate and cannot in any case be considered as representative for all areas and all seasons. However, the winters of 1957–58 and 1961–62 were unremarkable climatologically, and the figures obtained probably illustrate the general order of magnitude of losses likely to occur in normal seasons for spat more than 3- or 4-months old in the Crouch, and after metamorphosis on the Fal.

The distribution of the spat

The intensity and distribution of spatfall has long been of interest to ecologists, and attention has already been drawn to the differences in intensity of spatfall in successive seasons in the Crouch and Fal; however, in addition to changes in intensity there were changes in distribution.

In the Crouch in 1957, pre-settlement larval stages were present in the plankton continuously from 11 June to 12 August, with peaks in mid-June and early July. Spat were not measured but settlement had obviously taken place over a long period, judging from the differences in sizes of the spat. In 1958, a few pre-settlement stages were present in the plankton on 20 June, and on 14 and 21 July there were moderate numbers. Thus most of the spatfall would have been most likely in the latter short period and it was noted that the spat were more uniform in size when examined, though again no measurements were made.

The distribution of settled spat was quite different in the two years and the reasons for this are not easy to explain. In this context, it must be appreciated that in 1957 the larvae appeared sporadically for a longer period and were probably distributed by tidal action more evenly over the grounds than in 1958. In a brief spatting season the chance settlement of a group of larvae on one or other section of a plot could make a substantial difference to the distribution pattern.

In this experiment, the differently treated sections were along the long axis of the river and therefore larvae about to settle were presumably transported over one after the other. The beds upstream and downstream of Purleigh Shore were semi-derelict; therefore, if the larvae were settling on the ebb and flood and did exhibit some selectivity, they might have been expected to be more numerous on the cleaner, more favourable Purleigh Shore bed. However, this does not explain the greater intensity of settlement on the centre of the bed, unless there is a time-lag between searching and final attachment. The variability of the bottom (though this was unlikely to change much from one year to the next) and of the settlement surfaces available to the spat could partly explain the differential distribution of spat, but there was no real evidence that one section of bottom was less suitable than another.

Differences in the distribution of settled spat on the Fal were much more striking. In 1961, it appeared that either there was some fundamental difference in the character of the bottom on the west side, or that larvae were not present in the water in similar density on that side. The relative scarcity of oyster shells on the west suggested that this was a recurrent phenomenon but, equally, the relative paucity of suitable settlement surfaces could have prevented a build-up of oysters there. That availability of suitable settlement surfaces was a major factor was ruled out in 1961 by the presence of ample settling surfaces in the form of mussel shell in section 1, yet the settlement there was still only light. Thus it appeared either that there were fewer larvae in the water on that side, or that conditions such as scour or sedimentation rendered the area much less suitable for settlement.

However, spatfall was intense on the west side of the area in 1962, and this suggests that the low level of settling in 1961 was due to lack of pre-settlement stages in the plankton on that side, whereas in 1962 there was a plentiful supply and, with the increased cultch available, a correspondingly greater spatfall. The physical conditions on the bottom, correlated with the hydrographic conditions immediately above it, will have a bearing on spatfall but it has been established for many planktonic organisms that their distribution is patchy, with fairly well defined boundaries (Bainbridge 1953; Cassie 1959, 1963). If the distribution of planktonic oyster larvae, and particularly those about to settle, is patchy, then their settled distribution could also be so.

As an alternative, the suggestion by Nelson and Perkins (1930) and Carriker (1951) that the larvae are streamed by the tide, their activity varying with sudden changes in temperature or current velocity, could help to explain the localized set. They used this explanation of slicks to account for the subsequent appearance of bands of spat on the bottom.

In the River Fal experiments the settled spat were not measured, but from the variation in their sizes and from occasional plankton samples it was apparent that settlement

continued over a period of at least two weeks in both sons. This must have meant that the boundaries of the al swarms or the slicks caused by abrupt changes in rent velocity or water temperature must have persisted r a considerable number of tidal incursions, with an ence of larvae or uniformity of the water mass west of mid-line of the area in 1961. Even if the larvae at the -settlement stage were being replaced or replenished, they st have followed almost the same path each time. Accorg to Loosanoff and Nomejko (1956) minor currents are remely precise in their behaviour, and the present obserions support this.

A third explanation considered was that the different nbers of adult oysters in the various sections had contried to the variation in settlement. Mention has already n made of the trapping of larvae by adult oysters but re was no clear correlation between the numbers of adults r m^2 of bottom and the numbers of spat. There was howr a characteristic reduction in the mean numbers of spat tling on living oysters on the two western strips 1 and 2 1961 (Table 10).

It would seem that the patchiness of the larval distribution be a true and persistent feature of an estuary over fairly g periods (Nelson 1952). Such patchiness could be caused local hydrographic conditions (Carriker 1951; Cassie 59), by grazing by other planktonic animals (Bainbridge 53), or by the localized injection of large numbers of rvae into the circulation system (Knight-Jones 1952; augh 1954; Carriker 1951). If the third possibility is the se, and mixing and dispersion are relatively limited, then order to secure a more uniformly distributed spatfall it ould be necessary to have the stocks of oysters also unirmly distributed.

In this context, it is of interest that for many years few at had settled on the old shells dredged from Messack oint, yet they were perfectly suitable for spat collection, as evidenced by the settlement on them when they were reid on 2B and 6A. Presumably there were few larvae at the ttlement stage in the water off the point, for there was no idence that the shell or the conditions were otherwise nsuitable. Other sedentary organisms were plentiful on the ltch and there was no evidence of scour or silting which, Shelbourne (1957) pointed out, might interfere with spat tachment and survival.

Other areas of the Fal, notably the Vilt Bank in Falmouth arbour, which was once extremely productive, no longer rry a stock of oysters, yet to the north and west settlement good. Plankton surveys would show whether there are rvae in the vicinity of the bank; if there are not, then some distribution of breeding stocks could perhaps result in a nange in the distribution of the larvae.

he value of cultivation techniques

In the two series of experiments described, there was no crease in spatfall per unit area of the bottom that could be ttributed to harrowing. In both cases, harrowing, simply or the purposes of securing an increased spatfall, appeared be wholly uneconomic. Furthermore, as was shown in the rouch, intensive harrowing can have a detrimental affect n the growth of any oysters present. Nevertheless it is ossible that, in conditions where living oysters are partially uried in the substrate, harrowing will pull them out of the ottom and redistribute them on the surface, so preventing loss from smothering. In addition, harrowing during the run of the tide could eventually lead to the dispersal of mud which had accumulated over old oyster grounds. However, in this case, the economics of such an approach may be no more advantageous, or efficient, than the relaying of old cultch on the mud surface in order to re-establish the ground. On an already established ground, the dispersal of any small accumulations of mud is achieved in the normal course of working the ground.

The Fal experiment showed that if cultch is laid on areas where it is relatively scarce there can be an immediate increase in the catch of spat, provided that the shell is laid in an area where spat can reasonably be expected to settle. The experiment further indicated that the quality of the cultch is relatively unimportant, if the individual shells are not too small. Economically, mussel shell, if it is readily available, offers the best opportunity of catching spat, because it has a big surface area for its weight. The shells of *Chlamys*, too, offer good settlement surfaces, but they are less readily obtainable. Small shells less than about 6.0 cm^2 plan area are probably unsuitable and uneconomic as collectors. Any shell, not necessarily bleached but reasonably free of fouling organisms, will act as collecting material if it is dredged and relaid on the potential spatting ground.

On the Fal, underwater observations showed that the mussel shell laid in 1961 remained in very much the same position until autumn 1962, and the old shell laid in summer 1962 was also unchanged by the autumn. The most noticeable feature of this relaid shell was its irregular distribution and positioning. The shells had settled on the bottom at a variety of angles and presented many inclined surfaces to which spat could attach but which, because of their angle, did not collect silt.

The mussel shell laid in 1961 was only lightly harrowed to distribute it after relaying, but the old shell laid in 1962 was not disturbed and it seems probable that the absence of harrowing had contributed to its catching efficiency. Harrowing, although it may kill attached sedentary forms, has the effect of levelling the bottom and the shell on it. This reduces the variety of angles presented for spat attachment and also reduces the number of sheltered eddies in which crawling larvae can settle. Thus, on balance the dredging and relaying of shell offers a better chance of success in spat collection than does harrowing. The relaying of locally available cultch has obvious advantages, but care must be taken to avoid transplanting unwanted competitors or predators with it. This is illustrated by the accidental introduction of *Ocenebra* to the experimental area, where its presence could materially reduce the ultimate yield of spat from the ground.

Though there is a relationship between the yield of spat per unit area of bottom and the amount of cultch, there is nothing to be gained by laying too much shell; when present in excess it can be a disadvantage. Dredging to recover oysters laid amongst the mussel shell, after the experiment on the Fal was completed, proved laborious because the dredges quickly filled with shell which had to be sorted and the oyster catch per unit of effort was lower than on the other sections where shell was less plentiful.

onclusions and Recommendations

he experiments on the Rivers Crouch and Fal indicate the harrowing of grounds as a preparation for spatfall alueless, and that where there are stocks of oysters on ground the growth of these may be adversely affected.

redging and relaying shell offers a better chance of suc- in spat collection, and the addition of shell to relatively ren areas can be of positive value. However, because of variable distribution of settled spat, preliminary trials necessary to determine the areas in which cultch could aid to the best advantage. The type of shell used to catch t is relatively unimportant, provided that it is sufficiently shells with a plan area of less than 6.0 cm^2 (approxi- ely that of a two-year-old cockle) are of little value. able shells such as those of mussels offer the advantage t spat on them can be separated more easily and the ch is less likely to harbour shell pests.

he source of the shell is also relatively unimportant. If s not excessively fouled it can be relaid immediately, ing time in handling. However, if there is any danger of introducing fresh pests or predators to the potential spatting grounds, then the shell should either be searched very carefully or put on shore so that the pests will die before it is relaid.

Dense quantities of shell are of no advantage in normal seasons, though they may result in an increased catch of spat per unit area of bottom in seasons of heavy spatfall. It would be better to ensure adequate coverage over large areas of potential spatting ground than to concentrate shell in localized areas.

Seeding potential grounds with oysters does not seem to offer any advantage, but redistribution and concentration of stocks so that their larvae are released into different parts of the circulation of a large estuary like the Fal might be of help and result in the colonization of fresh grounds. The working of these by dredging, with its consequent lifting and relaying of shell, will be much more effective than harrowing in increasing the potential of the grounds for spat collection.

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